CROWN ARCHITECTURE AND

XYLEM-BORNE SUCROSE PRODUCTION IN

STAND-GROWN SUGAR MAPLE (Acer Saccharum Marsh.) OF THE

ADIRONDACK MOUNTAINS

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The concept of the ideotype is applied to trees grown for maple syrup production. While leaf area had been hypothesized as the controlling parameter it had not been actually measured, nor had individual tree yield been assessed on a per hectare basis.

Based on the hypothesis that leaf area and sap and sugar yield are causally related, a basic reassessment was conducted of both crown architecture and the temporal and spatial variation of xylem-borne sucrose production. Destructive sampling was conducted to measure above-ground allometry in 18 trees up to 43.5 cm dbh. Between 1981 and 1989, up to 86 trees were sampled for xylem sugar following several sap runs each year; of these trees, seven were open-grown and five were harvested at varying heights.

While crown volume was the best variable for predicting leaf area, it was not as effective as projected crown area or dbh in accounting for variation in sap and sugar yield among trees. Open-grown trees produced the largest amounts of sap and sugar, but when viewed on a per hectare basis, their yield was almost half of the maximum for stand-grown trees. Percent sap sugar was significantly

higher with increasing tap height, and while sap volume flow was greatly reduced, it did occur throughout the sap season, and without vacuum extraction, from single taps 14 m aboveground. Within year, the maximum recorded percent sap sugar appeared to coincide with the date at which the regression of the mean daily temperature raises above 0 °C.

Variation among years is clearly the largest source of variance in sap and sugar yield; however, previous defoliation studies indicate that xylem sugar and starch accumulation or photosynthetic capacity are not coupled. Research reported here supports this conclusion by showing a poor correlation of leaf area to percent sugar. Xylem embolization driven by leafless stem transpiration could be affecting sap yield and sugar concentration not only within the crown but also at breast height among different trees. Wintertime evaporative demand could, therefore, be more important than summertime photosynthesis in determining sap and sugar yield within and among seasons.

Biographical Sketch

Gabriel Frederick Tucker III was born a "Blue Devil" on August 12, 1952 in the Duke University Hospital in Durham, North Carolina. Later he was to be described as a "city boy forester", due to his formative years which were spent in Philadelphia "The City of Brotherly Love", with his family including four younger brothers and an older sister. He attended Germantown Friends School from grades 5 through 12 where he was particularly influenced by several creative science teachers including: Mr. Cadbury who in 6th grade thought him how to skin a squirrel and how not to skin a skunk, Mr. Platt who in 7th grade introduced him to concepts of sand dune stabilization, Mr. Purves who in 9th grade taught him to build bridges, Mr. Boles who in 10th and 12th grade taught him the facts of life on this planet, and Mr. Bassow who in 11th grade taught him of intellectual freedom guided by hypothesizes with some chemistry sprinkled in. Most of his education, however, has always been extra-curricular, including a summer spent as a 16-year old in Europe on an American Friends Service Committee Work Camp Program and, most memorable, "the summer of '69" when he attended Outward Bound in Colorado, worked as a Conservation Aide at the National Boy Scout Jamboree in Idaho, and then rode a bicycle home to Philadelphia. The trip took 33 days and cost $79 for the bike, a Schwinn Varsity which he still owns today, and $3 per day for food and camping fees.

As a high school senior, and after graduating in June of 1971, he worked as a laboratory technician for Dr. Mark Haussler who instilled in him forever a love of professional endeavor as a research scientist. He briefly attended the University of Arizona but soon transferred to Oregon State University where he enrolled as a freshman in the Forest Science Option of the School of Forestry under the guidance of Bill Ferrell. There he spent much of his time working within the International Biological Program's Coniferous Forest Biome where, under the tutelage of Steve Running, he learned the invaluable skill of mixing work and play by alternately taking measurements of plant moisture stress and fly fishing. Perhaps, most important was the influence of Bill Emmingham who helped bring an undergraduate thesis on conifer leaf morphology to fruition.

Within a month of graduating from college, in June of 1976, he entered the Peace Corps and was stationed as an extension forester in the village of Karaye in the remote Maggia Valley of the West African nation of Niger. Reenlisting twice as a volunteer he worked on several projects including projects in windbreak establishment, sand dune stabilization and a project to study wind erosion at the Niger National Agricultural Research Institute. He then worked for a period as a consultant to the World Bank on small-scale forestry after which he returned to the states after almost four years overseas.

Making his way back to the Pacific Northwest he landed upon fertile ground in the lab of Tom Hinckley, Professor of Tree Physiology, at the University of Washington in Seattle. There he worked with Jerry Leverenz on research relating to the shoot structure of conifers which lead to a Master of Science in Forest Resources completed in December of 1982.

Within two weeks of completing requirements for his degree he returned to Africa as a project manager for C.A.R.E. Working as a bush bureaucrat he spent a difficult two years in Cameroon and Mali learning to live without scientific inquiry. He did, however, manage to adsorb valuable experience within a formidable bureaucracy, particularly under, the patient but uncompromising guidance of C.A.R.E. Country Director, Felix Ashinhurst.

On August 10th 1984 he was married to Catherine Henshaw Knott in Koro, Mali with all of their parents attending. They returned to the U.S. at the end of that year and, after the birth of their son Joshua, they moved to Ithaca in May 1985 where they both started doctoral programs at Cornell - Gabe enrolling in the Department of Natural Resources in August 1985 and Cathy in the Department of Anthropology in August of 1986. In July of 1989 their second son Daniel was born and since then, life has only continued to get more interesting.

This dissertation is dedicated to Dr. Mark R. Haussler Ph.D.,

my first mentor,

whose generosity,

I will never be able to repay and

whose standards for research

I will always be endeavoring to live up to.

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A wide variety of individuals and organizations provided support for this research, without which it would never have been possible. It is impossible to name them all, notably the many maple syrup producers and others in the industry who, particularly early in my investigations, endured seemingly endless and inane questioning. To all of them, I am grateful.

At Cornell the staff and faculty of the Uihlein Sugar Maple Research-Extension Field Station were particularly helpful including: Lew Staats, John Kelley, Chris Moquin, Erma Rodriguez-Semp and Karen Fountian who provided literally years of patient and conscience logistical and field assistance. Lew and John were particularly helpful in providing insight related to the production of maple syrup and the maple syrup industry. Lew is also responsible for considerable data used in this dissertation which was collected prior to my arrival in May 1985.

During the summer of 1986, Steve Rice, a science instructor at Lake Placid High School, directed a 4-H Science Intern Program which brought four local high school students to work at the Uihlein Field Station. These students, Bob McBride, Weip Chen, Mike Rimlawi and Forrest Deitz, under Steve's supervision, worked for several weeks on what must have been, at times, very boring and tedious work. Their

hard work made it possible to develop the allometric equations upon which much of this research is based.

Generous financial support has been provided by Mr. and Mrs. Henry Uihlein II, as benefactors of the experiment station. The Kieckhefer Adirondack Fellowship Fund was also very supportive in providing two consecutive research grants in 1986 & 1987. In addition, research assistantships were provided through MacIntire-Stennis Forestry Research Funds and teaching assistantships through the Cornell Department of Natural Resources.

Some of the most generous assistance was provided by fellow grad students who unselfishly provided unending technical and moral support. Notably John Hayes, my office mate, who along with Cary Oshins provided significant enlightenment on the nuances of statistical analysis. Dave Cacela and Tim Volk who helped me down the long road to computer literacy, John Powell, who willfully risked life and limb in the collection of important data, and Bill Wischusen, Steve Siebert, Mary Arthur, Carola Haas, Jeffery Hughes and countless others, who constantly provided thoughtful feedback and advice regarding life on the 3rd floor and beyond.

The members of my graduate committee, including Chairperson Jim Lassoie, Brian Chabot and Tim Fahey, deserve special recognition, most importantly for their open willingness to listen. On many

occasions each of them would set aside other responsibilities and offer advise on yet another hypothesis. This contact was invaluable.

The staff of the Department of Natural Resources deserve special thanks particularly Betty Dempsey-Loid. She along with the others including Ellen Bowmaster and Deborah Walsh Grover helped to create the most supportive work environment that any graduate student could ask for.

Most important has been the encouragement provided by my family. Starting with the process of application to graduate school right through the dissertation revisions, Cathy has been extremely supportive by holding up the family life in general and on many occasions taking precious time to help with typing, spelling, and grammar. Josh and Daniel have sacrificed much also, particularly Josh who is now almost five-years-old. I will never forget once before my defense, when he was very sick, holding him in my arms I said "Josh, are you going to be alright?" and he said, "Daddy, I'm going to be just fine, but is your dissertation going to be alright?".

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PREFACE

This dissertation is composed of four chapters including an introductory chapter and a concluding chapter. A site description of the research area is contained in Chapter 1. Chapters 2 and 3 and appendix E are each designed to stand independently; therefore, a review of the pertinent literature is contained in the introduction to each of these sections. It is my hope that they will eventually be published as articles in appropriate journals; however, following collaboration with reviewers and co-workers, certain material will undoubtedly be removed and/or new material included.

Chapter 1: Research Context:
Introduction to the Dissertation

The overall objective of this dissertation is to provide basic scientific findings of interest to anyone concerned with the ecology and whole-tree physiology of sugar maple (Acer saccharum Marsh.) and associated species. At the same time, it is hoped that this work will find direct and more immediate application among those concerned with the production of maple syrup in the northeastern United States and southeastern Canada. To this end, one of the early tasks undertaken in this research was the systematic collection of information on the socio-economic situation and indigenous knowledge of maple syrup producers (Tucker and Tucker 1989a,b; see Appendix A).

During three consecutive years, starting in 1986, data were collected using a questionnaire which was distributed to all participating producers at the yearly New York State Maple Tour organized by the Cooperative Extension Service. The main objectives of this preliminary research were to: 1) develop a constructive rapport with practicing maple syrup producers by becoming more familiar with their professional concerns and management perspectives, 2) utilize their knowledge of the species to help develop specific testable hypotheses with both biological and socio-economic significance, and 3) collect information that would be

useful in garnering support from funding agencies and others.

One of the most interesting findings of this initial study was that while maple syrup production is often a minor component in the overall farm operation, it also frequently plays a crucial role in its economic viability. The successful small farm is becoming increasingly diverse, and maple syrup production is very often an important player in that scheme. When this perennial tree crop is used in conjunction with annual agronomic crops, maple syrup production is a good example of an agroforestry system and a important part of the increasingly recognized multi-disciplinary approach known as agroforestry.

As a forest tree ecophysiologist and an agroforester, one of the most encouraging aspects of this preliminary investigation for me was the realization that those working in the industry are not simply concerned with the raising of forests of sugar maple trees and the resultant products that they produce. More importantly, they are concerned with the health of the individual tree as a living biological system and all of the physiological ramifications that go with that. This is mainly because, unlike most other forest industries, the harvest of a sugar maple tree for its sap does not mean its demise. In fact, quite the contrary is true. Through careful management, the individual tree and the surrounding stand become even more healthy and continually tappable. In this sense the

harvest of maple sap, like other related operations in which trees are tapped for their exudates (e.g., rubber), can be seen as the epitome of sustainable agriculture.

All field work for this research was conducted at the Uihlein Sugar Maple Research/Extension Field Station near Lake Placid New York and is owned and operated by Cornell University. The experimental sugarbush where study trees were harvested is located at an elevation of approximately 610 to 671 m (2,000 - 2,200 feet) in the Adirondack Mountains on moderate slopes of generally easterly facing aspect. Soils originated from glacial till and are well-drained fine sandy loams of the Becket series (U.S.D.A. 1978). Forest vegetation in the study areas is dominated by sugar maple and American beech. Other species commonly found included: red maple (Acer rubrum L.), striped maple (Acer pensylvanicum L.), white birch (Betula papyrifera Marsh.), yellow birch (Betula alleghaniensis Britton), black cherry (Prunus serotina Ehrh.), pin cherry (Prunus pensylvanica L. f.), and balsam fir (Abies balsamea (L.) Mill.). Like most of the unprotected land in the area, this forest was probably logged heavily in the late 1800's or early 1900's, but since then it has been largely unmanaged and utilized only for maple syrup production and to a limited extent for firewood from dead and downed trees. During the last 20 years the site has been brought under more intensive management by selective thinning to promote healthy vigorous sugar maples for the production of maple syrup (Staats 1989,

personal communication).

The subject matter in this dissertation is divided into two parts, the first regarding the foliar and above-ground allometry of the species and the second regarding the variation of sap sugars as affected by foliar morphology and various other parameters. The first part is covered, in depth, in Chapter 2 and the second is likewise dealt with in Chapter 3. The overall hypothesis that guided the research presented here was that these two factors are causally related; that is, that whole-tree morphology, and in particular leaf area, dictates the quality and quantity of xylem-borne sucrose production in sugar maple. There is a large amount of empirical evidence from syrup producers (e.g., Tucker and Tucker 1989a,b), and scientific evidence from researchers (e.g., Morrow 1955) upon which this hypothesis is based. This evidence generally points to leaf area as being the limiting factor (see section 3.32), although leaf area per se had not yet been measured in relation to sap production.

Chapter 2: Crown Morphology and Above-ground Allometry

2.1 Introduction

The structure and function of forest canopies, like those of herbaceous plant communities, are closely related to their capacity for carbon fixation and primary productivity (Kira et al. 1969, Harper 1977). Light within the canopy is perhaps the single most difficult environmental variable to predict (Campbell 1981); however, both forest and herbaceous canopies follow the Beer-Lambert's law. This equation assigns light extinction coefficients based on the relationship between light intensity, relative to sun light in the open, and cumulative leaf area index (m^2/m^2) as one progresses through the canopy from above. Forest canopies tend to have much lower leaf area densities than herbaceous canopies (m^2/m^3) simply because of the very tall stature of trees. That in turn allows them to support higher leaf area indices and to be more productive than herbaceous plants grown under the same climatic conditions (Kira et al. 1969).

Interest has recently focused on crown morphology and biomass production for the individual tree in an attempt to better define ideotype tree crowns for possible genetic selection (Kuuluvainen and Pukkala 1987). Analyzing tree architectures of temperate zone conifers has shown that vertically extended, cone-shaped crowns are more efficient in stem biomass production than horizontally extended

umbrella-shaped crowns (Oker-Blom and Kellomaki 1982). This is reasonable because the between-tree shading is greatly reduced for stand-grown trees having tall narrow crowns (Kuuluvainen and Pukkala 1987). Furthermore, this is increasingly the case as one moves farther north to higher latitudes where the relative angle of the sun is lower. The opposite is true in the understory environment, here it is the species whose seedlings and advance regeneration saplings that display their foliage in a broad umbrella-like crown, to capture light coming from the zenith, which are at a distinct advantage (Tucker et al. 1987). In this way, the new growth is able to tolerate shade for extended periods of time to be positioned within the canopy hierarchy so that when a gap is created, canopy recruitment is possible. In broadleaf as well as coniferous species, this characteristic is important because it allows for selection cutting and uneven-aged management of forests using natural regeneration, a technique that is common in, for example, the hardwood forest types of the northeastern United states.

Temperate zone broadleaf species have received far less attention than conifers with regard to the selection and management of tree crop ideotypes based on crown morphology. The only exception is the hybrid poplar (Populus spp.) under intensive culture short-rotation systems (Nelson et al. 1981, Isebrands and Nelson 1981, Burk et al. 1983). In contrast, over 250 cultivars of sugar maple alone have been selected almost entirely on the basis of leaf and crown

morphology for applications in arborculture and ornamental horticulture (Santamour and McArdle 1982). Approximately 40 of these are commercially propagated and 10 have had been granted patents by the United States Patent Office. Sugar maple cultivar names like "Pyramidal", "Columumnare", and "Temple's Upright" attest to the importance placed on crown shape and form. To be sure, even the information in the official patent descriptions is not quantitative enough to enable even the crudest comparison of the clones. It does illustrate, however, that there is most likely very strong genetic control on the traits of crown morphology to produce vegetatively propagated individuals that are consistently characteristic and virtually identical as open-grown phenotypes.

The ecological significance of broadleaf tree architecture and its role in forest succession, has received considerable study including studies that have dealt specifically with sugar maple. Horn (1971, 1974, 1975) developed a predictive model of forest succession from empirical theory based on observations of the geometric leaf arrangements and soil moisture requirements of several forest tree species. From the point of view of tree architecture, perhaps most interesting was Horn's classification of tree species based on two categories of leaf arrangement: monolayered or multilayered canopies. Sugar maple was purported to be characteristic of the monolayered canopy. The theory then follows that the understory of such monolayered species will be characterized

by a conspicuous lack of new growth and the stand thus 'senile' (Horn 1975). Such a lack of understory regeneration is distinctly not, however, characteristic of sugar maple forests, which are known for their dense understories of abundant advance regeneration.

The parameter that has been most frequently used to characterize the canopy architecture of mature trees is the height of the live crown divided by the total tree height (live crown ratio). Holdaway (1986) developed a nonlinear model for 23 tree species in Minnesota, Wisconsin, and Michigan that predicted live crown ratio from the diameter at breast height (dbh; 1.4 m above ground surface) of the tree in question and the basal area per hectare of the surrounding stand. The equation for sugar maple was developed from 4,835 trees in northwestern Wisconsin and accounted for only 48 percent of the variation in the sample population (the overall range of species studied was from 13% to 89%). The behavior of the model though, for this and other species, was for the most part biologically reasonable. Conifers, for example, had much higher values for crown ratio at low basal areas than did broadleaf species which is reasonable in that open-grown conifers are often 100 percent live crown. This may also be related to the early successional, shade intolerant habitat of conifers in the study region in that the slope value related to this characteristic was almost consistently higher for the conifers while sugar maple, which is extremely shade tolerant, had the lowest value overall. In contrast, hardwood crowns

in general showed little response to competition in stands with higher basal area.

Live crown ratio together with crown diameter, has also been used to predict sap and sugar yields in sugar maple trees tapped for the production of maple syrup (Morrow 1955, Blum 1973). However, a step-wise multiple regression analysis did not yield consistent results. When models were developed, which accounted for as much as 79 percent of the variation, they showed poor correlation when verified with data from different years or different geographic locations (Blum 1973).

Allometric studies of sugar maple, and most other tree species, have focused on the biomass of the main stem and to a lesser extent on branch and total aboveground biomass of the tree (Ribe 1973, Whittaker et al. 1974, Goldsmith and Hocker 1978, Monteith 1979, Steinhilb and Winsauer 1976, Pastor and Bockheim 1981). This is due to the obvious economic importance of the bole as a source for high quality hardwood products and the role that branchwood and total aboveground biomass play in the calculation of primary productivity of the ecosystem (Whittaker and Marks 1975). Pastor and others (1984) have developed generalized equations based on several studies that use dbh as a predictor variable. The statistical errors of the generalized equations are within the errors of the equations from which they were developed and are purported to be applicable on sites

other than the ones for which the were developed.

Leaf area relationships for trees have been examined less frequently. The additional advantage of quantifying the area of photosynthesizing tissue and the origin of carbon fixation and net primary productivity must be weighed against the difficulty of such a task. Investigators in the Pacific Northwest and Japan have very successfully used the "Pipe Theory" (Schinozaki et al. 1964) to model leaf area based on sapwood basal area (Grier and Waring 1974, Waring et al. 1982) for a wide variety of species (Gholtz et al. 1976). Unfortunately these leaf area relationships, unlike those for woody tissues, discussed above, are not as generally accepted to be applicable from site to site (Whitehead 1987).

The only leaf area relationship that has been developed for sugar maple is based on dbh (Whittaker et al. 1974) and not the functionally and statistically preferable parameter of sapwood basal area. The use of sapwood basal area to predict leaf area of sugar maple is difficult because the boundary of the heartwood transition in this species is very poorly defined, which makes it very difficult to determine the cross-sectional area of xylem sapwood with the naked eye. Although heartwood transition does occur in sugar maple it is a gradual process over several years which is confined to the ray parenchyma and although the heartwood may be slightly darker in color the moisture content of the two zones is the same (Good et al. 1955).

Strong discoloration of heartwood often occurs, but this is invariably induced by wounding and not normal heartwood formation (see Kozlowski 1971a). Starch accumulated in living ray parenchyma elements of the sapwood can be stained using a iodine based dye (Wargo 1975), but this must be done with living tissue and only during the fall or early winter months before the starch is hydrolyzed into sucrose.

Microscopic examination of amber plugs, which characteristically form in the heartwood vessels of sugar maple (Laing 1953), could be used to delimit sapwood area. This technique would be difficult for measuring sugar maples that are tapped for xylem sucrose production, because the tap holes also induce the formation of amber plugs in adjacent sapwood and this could easily be confounded with heartwood formation and/or change the relationship of sapwood area to leaf area.

A reliable estimate of leaf area is important to the development of ideotype sugar maples particularly if the aim is to increase xylem-borne sucrose production. The primary productivity of the species is surely related to its leaf area and it would be difficult to maximize any type of dry matter accumulation without maximizing leaf area. Most importantly though, crown diameter, which must be closely related to leaf area, has already been shown to affect xylem sucrose production in the species (Morrow 1955, Blum 1973).

The main objective of the research, reported in this chapter, was to test the hypothesis that whole-tree, crown parameters of crown volume, and crown surface area could be used to predict total crown leaf area over a broad range of diameter classes and that this prediction would be more accurate than simply using crown diameter or dbh. An accurate estimate of leaf area is desirable to better characterize the growth habit of the species for the development of ideotypes for the maple syrup industry. Additionally, it was hypothesized that the gradation of light environments within the crown from the exposed upper canopy to the shaded understory was sufficient to necessitate the stratification of the crown to account for morphological differences of sun and shade foliage. A final aim was to test whether allometric relationships of wood formation along the main stem, which have been developed for conifers, would also be applicable for sugar maple.

2.2 Materials and Methods

2.21 Sample Tree Selection

The overall technique used to develop the allometric relationships was a modified version of the dispersed individual plant (DIP) method (Campbell and Norman 1989). During three weeks in

August 1987, 18 trees were harvested and analyzed for leaf area and aboveground volume of bark and xylem tissue. All trees selected, showed no outward signs of being deformed or unhealthy and two were taken from each of nine standard dbh classes ranging from < 5.05 cm (1.99 inches) to 40.64 - 45.69 cm (16.0 - 17.99 inches). One tree from each diameter class was from a stand that had been released through thinning, although not within the last five years, and the other was from an area which had been unmanaged, resulting in a denser stand. In addition, one tree in each dbh class over a tappable diameter (25.40 cm or 10.0 inches) had been tapped in the past and the other had not (see Appendix B).

2.22 Sample and Data Collection

Prior to harvesting, several nondestructive measurements were taken of both crown and whole-tree morphology (see Appendix C). These parameters included total tree height (th), height to the base of the crown (hcb), height to the lowest live branch (hlb), and height to the maximum diameter of the crown (hmd). Each tree crown was also measured for the total horizontal distance from the center of the bole at breast height to the vertical projection of the outermost point of the crown at eight compass bearings of 45 degree intervals starting at magnetic north. Height data were taken with a clinometer, and the crown parameters were also measured with the aid of prism based optical device designed for measuring the vertical projection of tree crowns (Jackson and Petty 1973).

In each case, the trees were felled with the stem being severed as close as possible to ground level. Once felled, the total length of the main stem and the height to the base of the crown were measured from the cut end (see Appendix C). The crown was then dissected into thirds by running lines perpendicular to the main axis at even intervals from the base of the crown to the top of the tree; thus, I divided the crown into upper, middle, and lower strata. All leaves were harvested and dried as quickly as possible to prevent weight loss due to respiration (Leverenz 1981, personal communication). In most cases, this was accomplished within 24 hours, but in the case of the two largest trees this process took approximately 48 to complete.

Wood disks were removed from the main stem and all branches at five levels throughout the tree, including: (1) the base of the tree just above butt swell; (2) breast height; (3) the base of the live crown; (4) the interface between the lower to middle, and (5) the interface between the middle and upper crown strata (Appendix C). All disks were air dried for six months at room temperature, after which each was measured to the nearest 0.01 mm with a digital caliper for both maximum and minimum dimensions to obtain an average diameter both inside and outside of the bark.

All leaves from each tree were harvested and bagged separately for each of the three crown strata, plus an additional level in the

cases where some leaves on epicormic branches were present below the main crown . A subsample of fifty leaves, selected at random (Jurik et al. 1985), was then taken from each of the three to four levels and frozen fresh to be analyzed separately as an estimator of stratified area leaf weight (Jarvis 1985) which is equivalent to specific leaf weight (Jurik 1986). These subsamples were each measured for total leaf area on a Li-Cor leaf area meter, bagged in kraft paper bags, and oven dried for a minimum of 48 hours at 71 °C. All remaining leaves were dried in the same manner and all samples were weighed to obtain stratified leaf weight for each of the 18 trees. Before weighing, seeds were removed from two trees in which some were present. Sugar maple characteristically produces abundant amounts of seed during seed years which come at three to five year intervals. The year 1987 was not a seed year, but these two trees did produce a small amount of seed particularly in their upper crown. The leaf weight data were then converted to leaf area using the area leaf weight (excluding the petiole) of each strata of each tree.

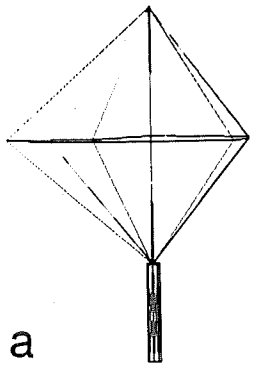
2.23 Data Analysis

A reconstructed or composite main stem was determined from cross-sectional areas of the wood disks that were removed at five levels throughout each tree. This was done to measure xylem and bark accumulation in a method that was comparable with other studies using taxa with a monopodial crown architecture characterized by a distinct, single main axis (Larson 1963).

The sum of the cross-sectional areas inside the bark was treated as a circular area from which a radius was derived to obtain the xylem radius of the composite main stem at a given level. This amount was in turn subtracted from the same calculation for composite main stem radius outside of the bark to obtain the bark thickness. The composite main stem volume was then calculated as the sum of five truncated cones from the summed cross-sectional areas and stratum height measurements taken after felling.

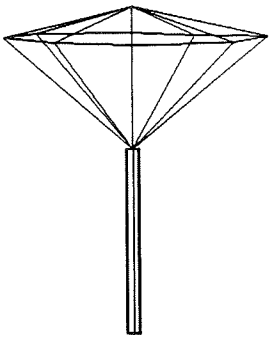
Crown volume and surface area were determined as those of two irregular pyramids, both with the same base as calculated from the eight crown radii measured prior to harvest. One of the pyramids was upright with its base at the height to the maximum crown diameter and its apex at the total height of the tree. The other pyramid was inverted with its base also at the height to the maximum diameter and the apex at the base of the crown (Fig. 2.1 and Appendix B). All height measurements used in crown and leaf relationships were taken prior to felling.

Figure 2.1 Three-dimensional crown architecture of four typical sample trees, one each from the four crown classes sampled. Crown volume is calculated with the projected crown area (b) determined from eight crown radii starting at magnetic north and crown depth determined from total tree height and height to crown base. The crown is then stratified based on additional pre-harvest measurements (a) including total tree height, height to maximum crown diameter and a height to lowest branch which may be below the crown proper (see methods).



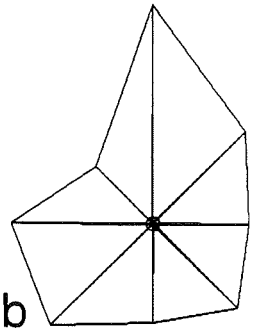
a

Dominant



a

Codominant



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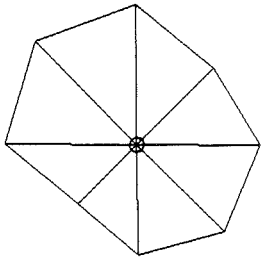

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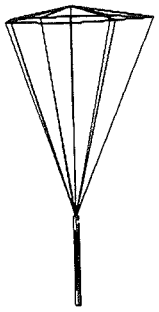
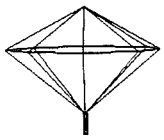


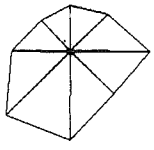
a

Intermediate



a

Understory



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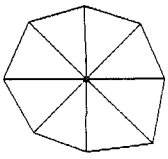


b

2.3 Results and Discussion

2.31 Allometry of Wood and Bark

The vertical distribution of xylem accumulation can be seen by means of the composite xylem radius (fig. 2.2a). All trees in the understory through codominant crown classes appear to have a relatively consistent taper of the composite main stem. The three dominant trees, however, show a distinctly different pattern with pronounced growth at the base of crown or between lower and middle strata. These differences are particularly pronounced considering the fact that at this level, especially in stand-grown trees such as these, xylem accumulation is for considerably fewer years than at breast height.

The vertical distribution of cambial growth in conifers has been well documented (Kozlowski 1971b) and contrasts markedly with what is reported here for sugar maple. Duff and Nolan (1953 and 1957) working with red pine (Pinus resinosa Aiton) developed several types of analyzes by measuring internodal length and radial growth of tissues of known ages along the branches and the main stem. Suppressed trees showed proportionally the largest amount of radial growth within the crown. The resultant main stem of such trees is very nearly cylindrical in form with little or no taper (Larson 1963, Kozlowski and Peterson 1962, Winget and Kozolowski 1965). With release after thinning, additional growth progresses downward on the

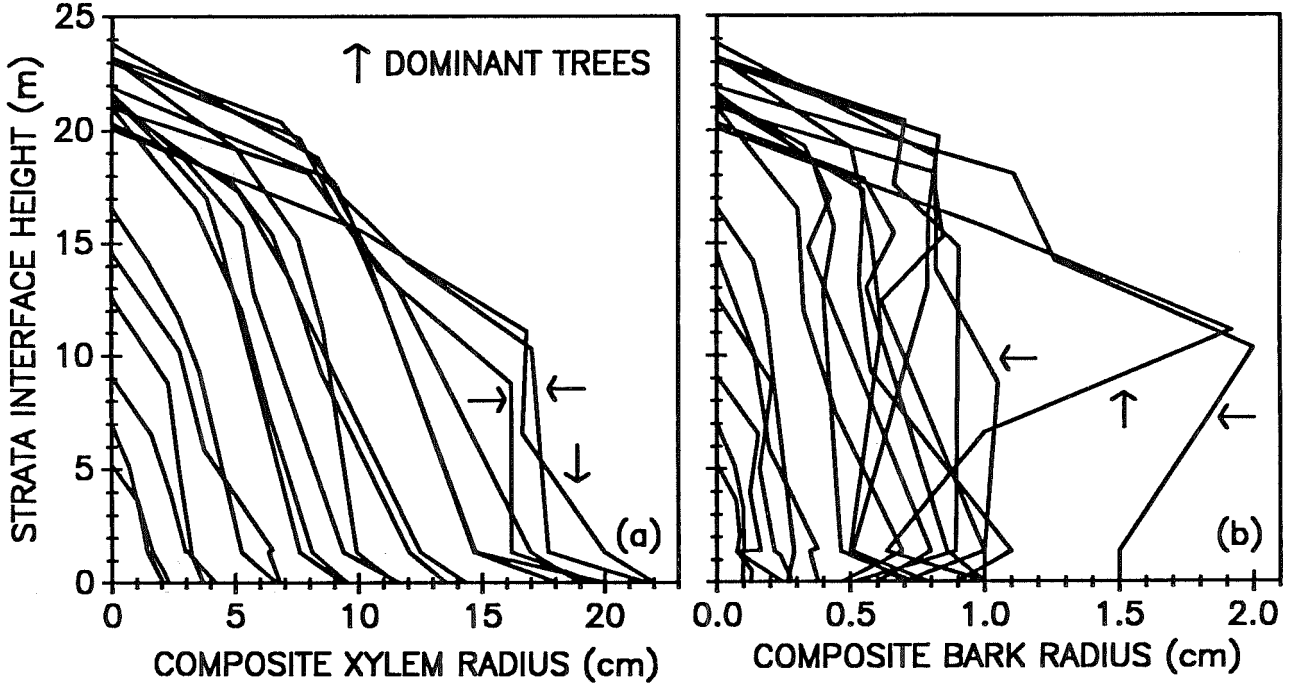


Figure 2.2 Composite radius of accumulated xylem (a) and bark (b) for the 18 sample trees at varying tree strata including the base of the tree, breast height, crown base and crown strata interfaces between lower and middle and middle and upper crown. Composite radius is derived from the total cross-sectional area of a given tissue at a given tree strata for each tree. Similar trends are evident for trees of all crown classes except the three crown dominants (see arrows above) which showed pronounced accumulation at crown base and/or interface between lower and middle crown.

main stem (Myers 1963) but codominant individuals continue to put on proportionally more radial growth within the crown (Larson 1963) and it is only dominants that each year accumulate the largest increment at breast height. In years of poor growth due to drought, the growth pattern of a given tree will shift toward that of a suppressed tree with increased growth in the crown (Smith and Wilsie 1961).

More recent work by Kuuluvainen (1988) discusses similar results with Norway spruce (Picea abies [L.] Karst.). It would appear that sugar maple is functioning differently than conifers in which it is the suppressed, intermediate, and codominant individuals and not the dominants that show patterns of increased xylem accumulation within the crown. Certainly it would be helpful to see the individual yearly increment in addition to the total xylem accumulation on these sugar maples and while the composite radius may not be exactly equated with similar data on xylem radii in monopodial species, the extent to which they are comparable shows a definite contrast with conifers.

The pronounced growth at the crown base and lower crown in these dominants may in fact be a result of reaction wood (Kramer and Kozlowski 1979) which could be produced to support broad cantilevered branching that is holding increasing amounts of foliage biomass. Fayle and MacDonald (1977), who studied the vertical distribution of growth layer profiles in three codominant sugar maples, found

similar, but less pronounced, growth in the single (non-composite) main stems that they examined. They attributed this observation to stem sway. There appears also to be a corresponding increase in bark accumulation (fig. 2.2b) which may be a side effect of increased cambial activity to produce reaction wood in the lower crown.

Bark accumulation, relative to total composite main stem diameter, appears greater throughout the crown than at the base of the tree and breast height. This is shown by the slopes of the regression lines (fig. 2.3) which have a highly significant difference (table 2.1, Sedecor and Cochran 1980). The equations with a log-log transformation (table 2.2) are better for actually predicting bark thickness because they yield the highest r^2. These could be useful, particularly at breast height, where the amount of diameter that is made up by bark is frequently considered. The proportionally greater amount of bark in the crown is probably due to the fact that these younger branches have not begun to shed as much bark as the older and larger main stem close to the ground. In addition, it may be due to the more horizontal nature of the branches that make up the composite stem diameter in the crown and the fact that they could accumulate more bark on the upper surface and/or in the presence of epiphytes. This bears significance also due to the possibility of stem transpiration (Milburn and Zimmermann 1986) causing winter desiccation and xylem embolism (Sperry et al. 1988) within the crown when the tree is in a leafless state.

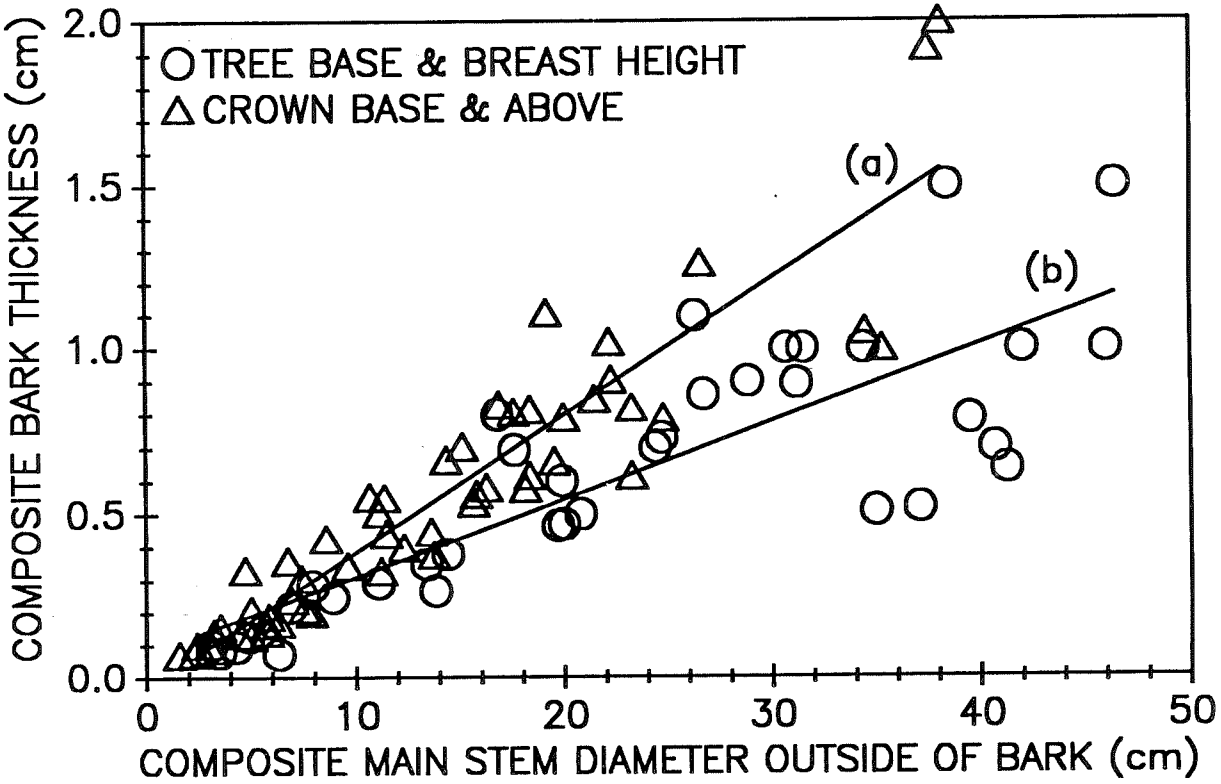


Figure 2.3 Composite bark thickness in the crown (a) and near the ground (b) as a function of composite main stem diameter outside of bark. Thickness derived from measurement of single main stem or bole near the ground and, in most cases, multiple stems in the crown. Proportionally thicker bark is evident from a F-test of the linear regressions (b, see table 2.1) of sample points within the crown.

Table 2.1 Results of F-Test of Untransformed Regressions of Bark Thickness and Leaf Area Above a a Given Crown Height

Statistic	Bark Thickness		Leaf Area	
	Elev.	Slope	Elev.	Slope
Fisher-Value	19.723	25.477	0.424	12.965
Degrees of Freedom	1,87	1,86	1,51	1,50
Probability	0.000	0.000	0.518	0.001
Figure/ Plots	2.3/ (a) vs. (b)	2.3/ (a) vs. (b)	2.6/ (a) vs. (b)&(d)	2.6/ (a) vs. (b)&(d)

Table 2.2 Allometric Equations for Sugar Maple Bark Thickness, Wood Volume and Leaf Area

DEPENDENT VARIABLE (Y) NAME	UNITS	INDEPENDENT VARIABLE (X) NAME	UNITS	FIG.	N	CONSTANT (A)	SLOPE (B)	STD. ERR. OF Y EST.	r^2
BARK THICKNESS AT BASE OR BH	cm	DOB AT BASE OR BH	cm	2.3b	36	-1.57	0.986	0.14	0.855
CMS BARK THICKNESS IN CANOPY	cm	CMS DOB IN CANOPY	cm	2.3a	54	-1.46	1.036	0.11	0.917
CMS XYLEM VOLUME	cm^3	DBH	cm	--	18	2.02	2.574	0.08	0.993
TOTAL CROWN LEAF AREA	m^2	CROWN BASE XYLEM CMS AREA	cm^2	2.6d	18	0.09	0.808	0.14	0.929
MID AND UPPER CROWN LEAF AREA	m^2	LOWER/MID CROWN XYLEM CMS AREA	cm^2	2.6b	18	0.17	0.804	0.15	0.931
UPPER CROWN LEAF AREA	m^2	MID/UPPER CROWN XYLEM CMS AREA	cm^2	2.6a	18	0.10	0.865	0.14	0.953
LEAF AREA ABOVE A GIVEN INTERFACE	m^2	XYLEM CMS AREA OF A GIVEN INTERFACE	cm^2	2.6c	54	0.15	0.808	0.15	0.936
TOTAL TREE LEAF AREA	m^2	DBH	cm	--	18	-0.01	1.434	0.19	0.873
TOTAL CROWN LEAF AREA	m^2	TOTAL CROWN VOLUME	m^3	--	18	-0.19	1.114	0.16	0.909

N.B.: ALL EQUATIONS FOLLOW THE FORM: LOG(BASE 10) Y = A + B * LOG(BASE 10) X

The extremely sensitive relationship (r^2=0.993) shown in the equation relating dbh to composite main stem volume (Table 2.2) is typical of many similar relationships developed for the prediction of woody biomass and volume (Pastor et al. 1984). The technique used here is, however, much more inclusive because, by using the composite radius to calculate truncated cone-like shapes at the different levels, it includes larger branches which are normally handled in a separate allometric relationship (Whittaker et al. 1974). The only component that is missing from this equation is smaller lateral branches which spread horizontally between strata interfaces (see Appendix C). This could represent a significant portion of volume of woody material in broadly branching open-grown crowns, but in these stand-grown trees even the finer branch material is mostly upright in orientation.

2.32 Crown Morphology and Leaf Area

The cumulative one-sided leaf area, for each of the 18 trees (fig. 2.4a), increased with decreasing stratum height at relatively similar rates for all trees until a threshold in the lower crown or below the crown, at which point almost all trees show a very sharp decline in leaf area accumulation. Only two trees did not conform to this general pattern and showed instead a more gradual decline and these were understory trees from unthinned stands. The slopes of the plots (fig. 2.4a) may actually represent the variation in leaf

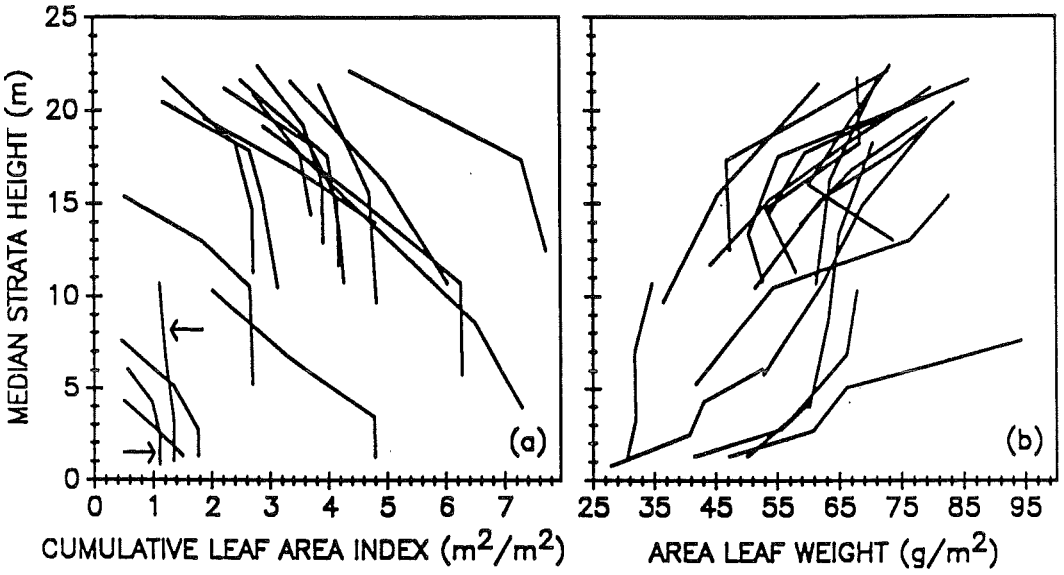


Figure 2.4 Stratified foliar morphology of the 18 sample trees including cumulative leaf area index with decreasing strata height (a) and area leaf weight (b). Both parameters include leaves on branches below the crown, when present. The endpoints and vertices in each plot indicate different crown strata. Those plots with four such points, indicate that the lower endpoint represents leaves present below the crown. Cumulative leaf area index increases at a relatively constant and similar rate for most trees to a threshold which generally coincides with the crown base or lower crown. The two understory trees, from unthinned stands, which were overtopped and suppressed (see arrows in above) had somewhat different plots indicating a larger proportion of leaf area in the upper crown. Area leaf weight (b) increased with increasing strata height in all trees except four overstory trees which actually showed proportionally heaver leaves in the lower crown and/or below the crown.

area density for the different trees. A steeper slope, therefore, would reflect a lower concentration of leaf area per stratum height, which would mostly be due to crown width.

The plots in figure 2.4a are somewhat analogous to stand light extinction curves (Kira et al., 1969), but for each individual tree because although one of the axes is stratum height in the tree instead of light in the stand, both variables decline with descending height in the stand. It is interesting, therefore, that the shortest understory tree accumulates its leaf area index at a rate very similar to even the largest dominant overstory individual. It appears that as long as an individual tree is able to receive at least some direct sun light and is not overtopped then it, as an individual tree, accumulates leaf area much as a pure stand would with decreasing light and plant height. Although, in this case, this may be somewhat due to the extremely shade tolerant nature of sugar maple.

Area leaf weight (leaf dry weight / one-sided leaf area) generally showed a steady decline with decreasing strata height within the crown (fig. 2.4b). This was true for all except four overstory trees that actually showed an increase at the lowest strata. That is proportionally heavier leaves are present in these trees in the lower crown and/or below the crown than at mid-crown. Area leaf weight (also known as specific leaf weight) is a indication

of the photosynthetic capacity of the leaf (Jurik 1986). Its increase with increasing light is probably due for the most part to increased leaf thickness caused by increased leaf tissues particularly palisade and spongy mesophyll which has been demonstrated for sugar maple and several other broadleaf and coniferous species (Wylie, 1951).

Huzulak and Elais (1975) studied foliar morphology of an individual of the closely related European species, field maple (Acer campestre L.) and also found declining area leaf weight with declining height in the crown. Their results however, did not show an increase leaf weight in the lower crown, but they did report smaller difference between lower and middle than between middle and upper crown. In addition, their definition of crown base may have differed and/or them may not have sampled below the main crown. The high area leaf weight observed for the lower crown and below the crown of four trees in this study may be due to increased light levels, particularly that of diffuse light, at lower levels in the stand than at mid-crown directly below dense foliage on the upper crown surface.

Mean crown radius was closely related to diameter at breast height (dbh)(fig 2.5a). This relationship would probably be more consistent if these were open-grown trees exposed uniform light and hence exhibiting less variation in crown radius. For example, Curtin

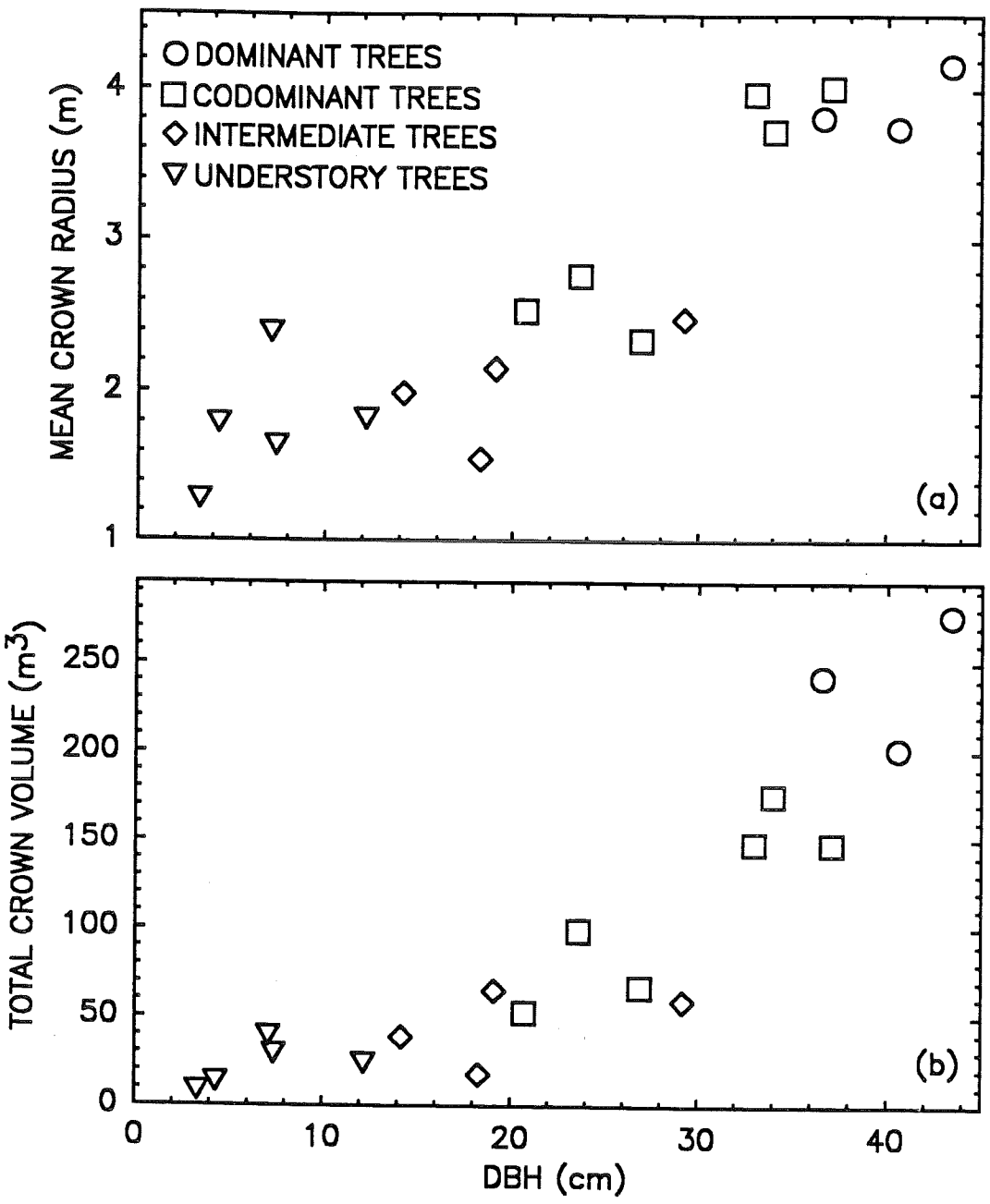


Figure 2.5 Mean crown radius versus diameter breast height outside bark (a) showed more variation than a similar plot of total crown volume (b). This may be due to an increase in sample units (i.e., eight radii per volume) but crown volume was consistently highest in dominant trees.

(1964), working with open-grown messmate (Eucalyptus obliqua L'Herit.), developed a very tight statistical relationship yielding a r-value of 0.984 without any type of log transformation. With these stand-grown trees, it appears that total crown volume is better predicted by dbh than is mean crown radius (figs. 2.5a,b).

The crown parameter of ultimate interest is, of course, total leaf area, and dbh appears to be moderately good at predicting this as well (table 2.2). This relationship has been studied by others and has practical as well as biological significance in that dbh is the easiest and most accurately measured of any tree dimension. Whittaker et al. (1974) developed several predictive models using dbh for sugar maple including total leaf area that yielded extremely significant statistical results. The measure of statistical error in the results reported here are much more similar to those reported by Jurik et al. (1985) for red maple.

The cross-sectional composite xylem area within the crown could be a good approximation to sapwood area at that level. This is because in contrast to breast height there is relatively little heartwood that has formed within the crown. Hence, the vast majority of the xylem should be sapwood and indicative of the leaf area above a given level in the crown. Although, it is not easily measured, it could be of interest from a more purely ecophysiological standpoint. Figure 2.6 is a series of plots of leaf area above a given stratum

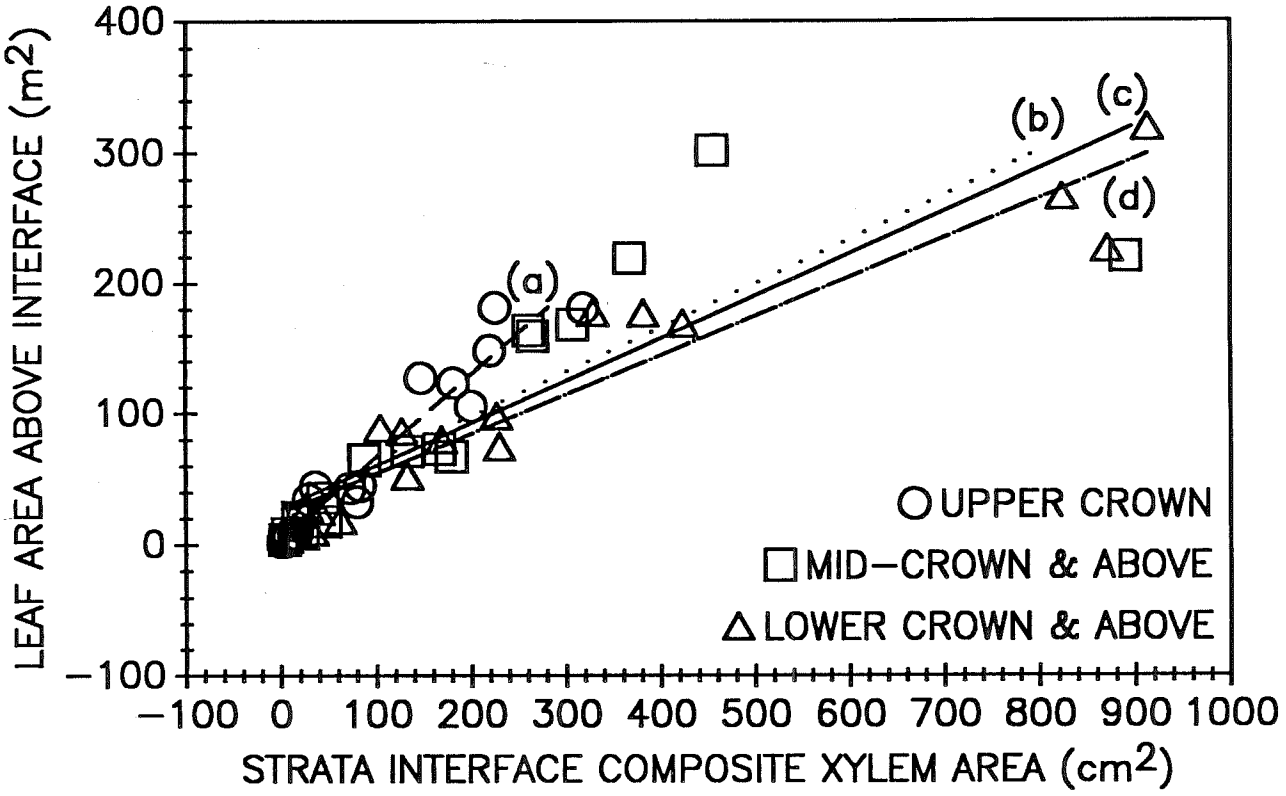


Figure 2.6 Leaf area above a given crown strata interface as a function of the composite xylem cross-sectional area of that interface. The plot of upper crown leaf area (a) showed a distinctly steeper slope than other plots (see tables 2.1 & 2.2) followed by mid and upper crown leaf area (b), regression of all points (c) and finally the plot for total crown leaf area versus crown base xylem area (d).

interface versus the cross-sectional composite xylem area for that interface. The plots for the two lower interfaces, and the line representing the regression of all the data points, show very similar slopes whereas the line for the upper crown alone is distinctly steeper (fig. 2.6). The slope of this line has a highly significant statistical difference (Snedecor and Cochran 1980) from the slope of the line formed by all the other points (table 2.1). This is plausible due to the decreasing branch and composite main stem diameter and proportionally higher leaf areas in the upper crown to utilize the direct sunlight of the upper canopy surface. It also means, however, that water supply to these leaves is relatively lower. Sun leaves of other species, particularly conifers (Tucker and Emmingham 1977), have been shown to have a relatively larger number of stomates of a reduced size that could result in increased stomatal control of transpiration.

Total crown leaf area density as related to mean radius appears to be lowest for understory trees or at least for three of the five individuals of that crown class (fig. 2.7). Individuals in the other crown classes varied widely although the dominant and intermediate trees showed some clustering in the plot. Research on conifers (Kuuluvainen 1988) showed an increase in leaf area density with declining crown radius. This is conceivable in that narrow crowned suppressed or intermediate conifers with increased xylem accumulation, as discussed before, should in turn have increased leaf

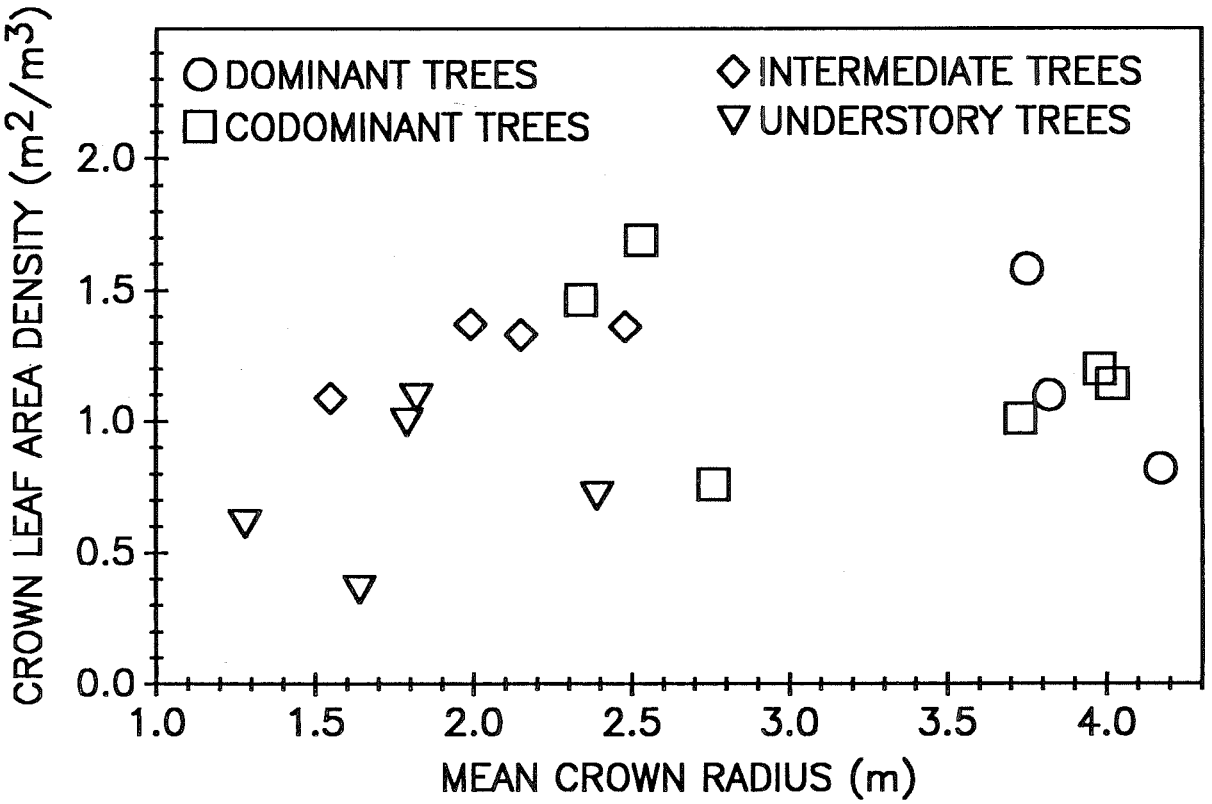


Figure 2.7 Total unstratified leaf area density versus mean crown radius varied widely for trees of all crown classes although understory trees tended to be lower. The highest densities were found three overstory trees (two codominants & one dominant) which differs from similar data on conifers which shows highest densities in intermediate and suppressed trees.

area densities to utilize all available canopy light and maximize growth to emerge from competition or suppression. This work with sugar maple does not confirm these results, and in fact, if any trend is present, it is the opposite: increasing leaf area density with increasing crown radius and increasing crown dominance. This contrast may once again be due to the extreme shade tolerant nature of sugar maple and also that the conifer stands studied may not have had understory trees and/or they may not have been included in the analysis.

Crown volume of individual plant canopies is most often approximated as being ellipsoidal (Campbell and Norman 1989, Charles-Edwards and Thornley 1973) although other shapes have been used such the cone for stand-grown conifers (Kuuluvainen and Pukkala 1987) and the prolate spheroid for orchard grown citrus (Turrell 1961). All of these shapes assume a convex crown surface in at least the horizontal plane. The crowns of stand-grown, broadleaf trees, particularly shade tolerant species, do not conform to this assumption. Concave neiloidal crown surfaces are perhaps equally as common in, for example, unthinned stands where the branches of several trees extend horizontally in competition for light from a single canopy gap or in thinned stands where epicormic branching extends crowns vertically downward along the bole. For this reason a multifaceted double-pyramid crown shape was used (see methods) that assumes neither convex nor concave surfaces but allows for both through multiple

measurements of crown radius.

The limitation of this shape is that it assumes a linear reduction in crown radii above and below a single height and because of this it tends to underestimate the volume of columnar shaped crowns; however, in closed stands, columnar crown shapes are uncommon. Vertically extended crowns are most often fan or vase shaped which, in general is well approximated by this method, although in some cases they are also underestimated particularly for intermediate and understory trees. A stratum-by-stratum examination of leaf area density, and its components of stratum volume and leaf area, illustrates this point. Within-tree leaf area density is highest in the upper stratum of taller trees and in the lower stratum of shorter trees (fig. 2.8a). While the high levels in the upper strata are quite clearly due the high leaf areas at that level (fig. 2.8b), those in the lower stratum of the shorter trees may frequently be due to the extremely low stratum volume estimates in those trees at that stratum (fig. 2.8c).

When calculating unstratified total crown volume, the measurement of the height to the maximum crown diameter (i.e., the height to the base of the two pyramids that form the crown [hmd], see Appendix C and fig. 2.1) is of no significance. This is because, algebraically, only the crown depth (tree height minus crown base

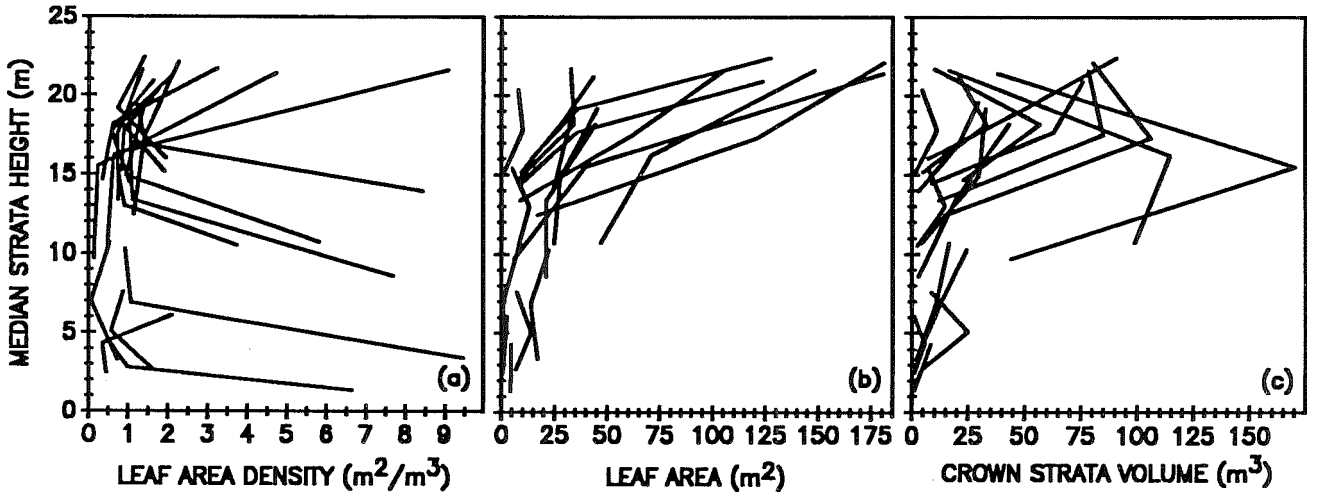


Figure 2.8 Stratified leaf area density (a) and component parameters of leaf area (b) and crown strata volume (c) for upper middle and lower strata of 18 sample trees. Leaf area density (a) was generally lowest in the middle stratum which also had the highest stratum volume (c) in 10 of the 18 trees while stratum leaf area (b) was the highest in the upper strata of several overstory trees.

height) and the projected crown area (calculated from the octagon formed by the endpoint of the eight radii) are need to calculate crown volume. The volume of the crown calculated as a single irregular pyramid (1/3 times the base [pca] times the height [crown depth]) is equal to the volume of the two component pyramids using the same base. Even if sapwood basal area could be measured in sugar maple with multiple increment cores, it might be easier and certainly less destructive simply to measure the eight crown radii and crown depth to obtain an estimator of leaf area.

While one should be hesitant to draw conclusions based on estimates of stratum volume, particularly those for the lower stratum of smaller trees, the estimates of total crown volume are very consistent and statistically significant. This point is made by the regression of total crown leaf area versus total crown volume (table 2.2). This relationship is statistically highly significant with the linear regression of the log transformations for both axes accounting for 91 percent of the variation (table 2.2). Only 87 percent of the variation is accounted for by a similar relationship using dbh so clearly crown volume is the best predictor of total crown leaf area revealed by this study.

2.4 Summary and Conclusions

The allometric parameter of total crown volume appears to be a good predictor of total crown leaf area in sugar maple and may be useful in other species as well. The relationship shows less variation than one which uses simple dbh as the predictor variable to estimate leaf area. Although crown parameters are more difficult to asses than dbh, the relationship should prove useful for research purposes in that sapwood basal area, which is the only other parameter which has been shown to be better than dbh, is impractical to measure in this species.

The composite radius of multiple stems at different strata within the crown also appears to have possible application in defining allometric relationships in sugar maple and other hardwood species. It would be useful, however, to examine this parameter on the basis of yearly increment and to compare it with more established techniques for estimating whole tree woody biomass and volume.

Distinct differences are evident in the morphology of sun and shade foliage, which confirms work with other species and highlights the need to stratify the crown when making any estimates of foliage surface area or biomass. These results were not, however, without some new findings. Most interesting was perhaps, the increase in area leaf weight (i.e., proportionally heavier leaves) at the lowest

stratum level in several trees. These were mostly on epicormic branches and may indicated that they are functioning physiologically different than their counterparts within the crown. This may also be a result of the extremely shade tolerant nature of sugar maple and could also have practical significance if it enables the species to respond to thinning via epicormic branching and increase leaf area and net production.

The xylem accumulation and foliar morphology of sugar maple does not completely conform with several reports on similar aspects of conifers. This is logical given the striking morphological and ecophysiological differences between these two plants taxa. Conifers, as a group, are distinctly monopodial with inherently more apical dominance and less shade tolerance. If one is to develop ideotype deciduous trees that follow the conifer model (i.e., having conical upright crowns to maximize light interception per land area occupied) then it will almost certainly be confined to even-aged plantations. While this approach may be extremely useful in an intensive culture, industrial setting it may be less useful under constraints demanding low input. In such situations, it may be more useful to capitalize on the morphological diversity of an indigenous gene pool and promote growth as an uneven-aged stand with trees that respond to thinning with abundant epicormic branching and regenerate in the understory as broad crowned shade tolerant advance regeneration.

Chapter 3: Spatial and Temporal Variation of Xylem-Borne Sucrose Production

3.1 Introduction

The xylem tissue of woody dicots is most often considered for its structural properties in supporting a foliage canopy, and as a pathway through which water and nutrients move to transpiring leaves (Long et al. 1981). It is now becoming clear that in certain species, such as several members of the genera Acer, Betula, Salix, and Populus, xylem vessels function as a pathway for carbohydrate. Sugars are loaded into xylem vessels via contact cells in ray parenchyma through an active metabolic process for storage or for transport over relatively long distances to other parts of the plant (Sauter 1980, 1981). This role, as a pathway for carbohydrates, is one that is generally reserved for the sieve tube elements of the phloem. Xylem-borne carbohydrate, which is usually in the form of soluble monosaccharide and disaccharide sugars, is thought to serve to initiate springtime flowering and shoot growth (Sauter 1980, 1981) when the plant is still in its leafless state, perhaps before the phloem is fully functional.

Whereas water and nutrients in the transpiration stream are lifted to the canopy by the cohesive forces of water molecules (Zimmermann and Brown 1971), the water and soluble carbohydrates in

the early springtime xylem sap must be transported through some form of positive pressure because of the leafless state of the tree and the general absence of transpiration. Positive pressure is necessary because, as Tyree and Sperry (1988, Sperry et al. 1988) have recently demonstrated, at this time of year the minor branches are embolized. Wintertime stem transpiration, which may be the main cause of this embolization, has been demonstrated in sugar maple by Milburn and Zimmermann (1986) using potometers. It may be hypothesized that the positive xylem pressure, which has been so well documented in sugar maple (see Tyree 1983), mainly functions to restore moisture to the transpiration stream and to provide soluble carbohydrates to the crown for the initiation of flower and/or shoot growth in the spring.

In the case of Betula, this positive pressure is in the form of root pressure generated by osmosis (Kramer and Kozlowski 1979). The Aceraceae, however, seem to utilize an entirely different mechanism. Milburn and O'Malley (1984) demonstrated that this process is probably driven by the formation of ice on the inner walls of the xylem fibers which compresses gases within the lumen creating pressure that is released with the subsequent thawing of the xylem.

The phenomena of xylem-borne sugar and positive xylem pressure form the basis of the maple syrup industry. Over the years, several major papers have been published that describe various aspects of sap and sugar yields of individual trees and tap holes (Jones et al.

1903, Jones and Bradlee 1933, Taylor 1956). This early research was limited because it preceded modern statistical methods utilizing error estimates, and because sample sizes were often small. More importantly, the entire industry, as well as research and development groups, have until recently concentrated production on the higher yielding and more accessible open-grown trees, including those growing along roadsides or in more park-like and open sugarbush settings where the number of trees per hectare was rarely a concern. This emphasis is largely due to sap collection methods. Until the relatively recent introduction of plastic tubing, each individual tree had to be accessed several times each spring to harvest the sap by hand. The sap was then transported by horse or tractor to the sugar house for processing. Trees on upland sites that were either too steep and/or too dense to be accessed were simply left untapped. Increasingly, these relatively dense and often previously unmanaged stands are being brought into production. However, one of the most basic concepts of modern forest management has yet to be addressed in maple sugarbushes -- stand density. Principles of individual tree production that were developed for open-grown, park-like sugarbushes may be less important in denser, closed stands, particularly if yield is viewed on a per hectare basis, as opposed to the per tree or per tap basis which has been the research and industry norm to date.

The object of this chapter is to assess sap and sugar yield on the individual tree basis, while at the same time considering the

density dependent factors, or spatial costs, that the producer must accrue to harvest that yield. In addition, it is important to relate these results to recent findings that have helped to present a more complete picture of the ecophysiological processes that control tree function and sucrose yield both throughout the year, and from year to year. In short, it is hoped that a modern reassessment of individual tree sap and sugar yields can be presented -- discussing variation within tree, among trees, within, year and among years.

3.2 Materials and Methods

Meteorological data for this study were recorded at the field station during the spring sap season each year (approximately March through April; hereafter referred to as the sap season). Air temperature was recorded with a chart recording thermograph (Weather Measure Corporation, Sacramento, California) mounted in a standard weather shelter located within the experimental sugarbush and supplemented by maximum/minimum air temperature, which was observed daily throughout the sap season at the station office. Additional maximum/minimum air temperatures were also obtained from a U.S. Weather Service Station, which is maintained by the Department of Plant Pathology, Cornell University, at the Cornell-Uihlein Farm directly adjacent to the sugar maple field station.

3.21 Sampling of Xylem Sap

Measurements of xylem-borne sucrose were made on individual trees throughout the sap season during the years 1981 to 1989 (see Appendix D). Trees were tapped at the beginning of each sap season with a 0.79 cm (5/16 inch) drill bit, to a standard depth of 7.62 cm (3.0 inches). Moderately conservative guidelines (Buzzell 1987, Coons 1987) were used for tapping: trees 25.4 cm (10 inches) dbh to 43.2 cm (17 inches) dbh received one tap; those 43.2 cm (17 inches) to 70.0 cm (24 inches) received two taps; and those 70.0 cm (24 inches) to 76.2 cm. (30 inches) received three taps. Trees that received a single tap hole were tapped in the same quadrant with regard to the cardinal compass directions each year. Trees receiving multiple taps were bored at approximately even intervals around the main stem. Immediately following drilling, tap holes were disinfected with a 5 percent solution of chlorine bleach. Sap was collected through a standard plastic spile and plastic tubing (Lamb Tubing Co., Bernard's Bay, New York) to a 18.93 l (5.0 gallon) food grade plastic bucket. To minimize evaporation, the tubing passed into the bucket via a tightly fitting hole in the upper side, and each bucket was covered with a plastic lid fitted with a rubber gasket. Following each collection period throughout the sap season, all buckets within a given sampling group were measured sequentially, usually within one to three hours. Sap volume was measured in the field with a graduated cylinder with maximum error in all volume measurements less than 5 percent.

3.22 Within-Tree Variation

Intra-tree variation in the quality and quantity of xylem sucrose were measured in three separate experiments on five trees for which sap records had been maintained since 1981. The first experiment conducted in 1987 measured sap production from within the canopy and at approximately breast height (two taps per tree). In 1988 the trees were tapped at mid-bole or just below the limit of the hydrostatic pressure head and also at approximately breast height (two taps per tree). Finally, in 1989, a control experiment was performed to measure yield from the canopy height tap holes, similar to 1987, but without the possible interacting effects of the lower tap (i.e., each tree received only the one tap). As additional controls, five trees were selected at random from trees in the medium intensity thinning plot (see Appendix D), which was most representative of the environment of the five trees. Data from these trees was, therefore, used as comparable breast height yield.

In 1981 (see appendix D), the five trees were selected as being representative of other trees in the experimental sugarbush (this sampling group is hereafter referred to as the five trees). Each of these five trees was located in areas that, like most of the sugarbush, had undergone a moderate thinning to promote tree growth and sap production. The same five trees were successively tapped, with a single tap hole, each year through 1986 at the standard level of approximately breast height. Beginning in 1987 these trees were

tapped above this height to sample xylem sucrose content at different levels in the tree. During the 1987 sap season each tree received two taps: one near breast height (approx. 1.4 m or 4.5 feet), and the other at an average of 13.8 m (45.25 feet) from ground level. The upper taps were within the tree crown, along the main stem of the tree, at a mean diameter of 21.1 cm (8.3 inches) and a minimum diameter greater than 20.0 cm (7.9 inches). The canopy of the trees was accessed for tapping using modified, direct-aid rock climbing techniques (see Appendix E). The actual tapping, sap collection, and measurement for the upper and lower taps were identical except that the upper tap had a much longer length of tubing between it and the collection bucket on the ground. During the 1988 sap season, sap was collected from taps at breast height and at mid-bole, at a mean height of 7.8 m (25.5 feet) above the ground, and a mean stem diameter of 28.8 cm (11.3 inches). Then, during the 1989 sap season, the trees received a single tap within the crown, similar to the upper tap during the 1987 season.

3.23 Thinning Experiment and Open-Grown Trees

Starting with the 1986 sap season, trees were tapped in an area that had been set aside as a thinning experiment in 1967 (hereafter referred to as thinning plot trees; see Appendix D). Stands were thinned to two different intensities plus a control and from 1967 to 1985 the trees had not been tapped. In this study each tree is

treated individually regardless of thinning treatment. During the 1986 season 15 trees were selected as representative of each treatment and tapped for a total of 45 trees. In 1987, the number of thinning plot trees was increased to include all trees which met the tapping guidelines (see above); the trees were measured yearly to the nearest 0.3 cm (0.1 inch). In 1988 and 1989 the tapping guidelines were interpreted in a slightly broader sense, in order to be more representative of actual practices within the industry, by measuring trees yearly but only to the nearest 2.54 cm (1 inch) instead of to the nearest 0.3 cm (0.1 inch). Each year, additional taps were added as more trees grew to a tappable diameter and/or large enough for multiple taps. By the 1989 season, a total of 78 taps and 73 trees were contained in this sampling group (see Appendix D).

The final sampling unit was started in 1987. It was located in an open-grown meadow site (see appendix D) on the Heaven Hill Farm operated by Mr. and Mrs. Henry Uihlein II directly adjacent to the sugar maple station. The stand was composed of two single stem dominant trees which were large enough to receive three taps each, plus two groups of trees exposed on at least two sides, similar to roadside or fence-row groupings of open-grown trees.

In addition to xylem sucrose measurements, each of the above-mentioned trees was assessed for whole tree dimensions, crown morphology, and stand point density during August of 1988. The tree

parameters included total tree height and dbh. In addition, crowns were analyzed based on eight independently measured crown radii, which yielded a measure of projected crown area (pca) and crown volume (for complete details see Chapter 2). Point density was measured using a standard timber cruising prism with a basal area factor of 20, which yielded a measure of stand basal area per acre surrounding each sample tree. This was then converted to total stand basal area per hectare by adding the basal area of the tree in question, and converting to metric units.

3.24 Measurements of Sap Sugar

Refractometer measurements were used at each collection period to assess xylem-borne sucrose collected from each separate tap. During the 1981 to 1987 sap seasons, measurements were made in the field to the nearest 0.1 percent dissolved solids using a hand held temperature-correctable refractometer. Several models of refractometers are available and one with a 0-10.0 percent scale and an accuracy of 0.1 percent was found to be most satisfactory (e.g. those manufactured by Atago Inc. and distributed by Cole-Palmer Inc., Chicago, Illinois, U.S.A.). During the 1988 sap season the procedure was improved by the addition of a temperature compensating, benchtop refractometer (Mark II Model 10482, Reichart Corp. Rochester, New York, U.S.A.). Samples were collected in the field using 100 ml glass scintillation vials with plastic sealed caps and

measured as soon as possible in the station office. These measurements are also accurate to 0.1 percent, but the automatic temperature compensation allowed for more reliable precision and, in addition, it was possible to perform a set of volume measurements much more rapidly. Regardless of the type of instrument used, three important precautions were always taken: 1) the sap solution was well stirred and homogeneous with no ice, 2) care was taken to keep the collection vessel and the refractometer clean and free of contamination, and 3) data or measurement techniques were adjusted to compensate for changes in air temperature.

Gregory and Hawley (1983) used colorimetric methods to identify the soluble constituents of the springtime xylem sap of sugar maple and found over 99 percent sucrose, and minute amounts of other soluble compounds but never more than 0.05 percent reducing sugars. They recommended that, because the refractometer readings so closely approximate the colorimetric percent sugar concentration ($r^2 = 0.99$), the readings can be considered as measures of sap sugars. Hence, units used here conform to the convention of equating sap solute to sap sugar or xylem-borne sucrose.

3.3 Results and Discussion

3.31 Within-Tree Variation

Past research on the variation of xylem-borne sugars within individual sugar maple trees has most often considered the effects of varying the orientation and number of tap holes. For a tree of any given diameter, the total sap volume yield increases with an increasing number of taps, but the yield per tap decreases (Morrow 1963). This would indicate a certain degree of interaction between tap holes. This potential interaction appears, however, to be affected by the relative position of the tap holes due to the very small amount of lateral, as opposed to longitudinal, movement of sap. Experiments using dye to follow sap movement have shown that even negative pressure has little influence on yield from tap holes, as close as 2.54 cm (1 inch) to each other, that are at the same height on the bole. This contrasts sharply with the longitudinal zone of influence, above and below a tap, which is at least 10 to 20 times that distance (Blum and Koelling 1968). The lateral interaction between tap holes, therefore, involves more the exchange of gases and/or their associated pressure whereas the longitudinal interaction involves more the actual sap moving from the vicinity of one tap to another.

The effect of tap aspect with respect to compass direction was one of the earliest concerns of researchers. Jones et al. (1903)

found only a slight increase in sap flow from the south side of relatively open-grown trees, which was attributed to increased solar radiation. Very few other results have been reported in the literature regarding aspect of tapping. Although Gregory and Hawley (1983) did take aspect into consideration when they measured changes in sugar content with time, they did not report on it. They measured percent sap sugar soon after tapping, and then 60 minutes later at the four cardinal directions on 15 trees. I reanalyzed their results by ranking (4=highest, 1=lowest) the four directions for each of the 30 measurements, that yielded the following mean ranks and 95 percent confidence intervals: north was 2.56 +/- 0.34; east was 2.60 +/- 0.37; south was 2.50 +/- 0.38; and west was 2.33 +/- 0.44 (see Appendix F). Clearly, there is no significant difference, at least in the relative ranking, among the sap sugar contents of the different aspects.

Xylem age, however, has been shown to have a very important effect on sap and sugar yield. The outer younger wood contains the highest sugar content, which is negatively correlated with xylem age up to approximately 55 years, at which point the curve levels off (Gibbs 1969). Sap volume yield, on the other hand, is positively correlated with xylem age until approximately 35 years, at which point it drops off (Gibbs 1969). Gregory and Hawley (1983) also measured sap sugar content in one- and two-year-old shoots of open-grown trees near ground level, and from taps along the main stem of

the same trees at a height corresponding to the shoot height. They found that, while there was no significant difference with shoot age, sap from the shoots did tend to be slightly lower in sugar content than sap from the bole. They suggested that this situation may reverse in late spring when sugar is mobilized to metabolic sinks in branch apical meristems.

Far less attention has been given to intra-tree variation of sap parameters at markedly different heights within the tree. In this research, as hypothesized, xylem sucrose content of sap from the upper taps was greater than from taps at breast height although volume yield was greatly reduced. In 1987 and 1989 (figs. 3.1b and 3.3b) the percent sap sugar from the crown was significantly higher (at alpha = 0.05). In 1988 (fig. 3.2b) at a reduced height, the percent was also consistently higher, although the difference was not statistically significant. The control experiment which was conducted in 1989 was done with the hypothesis that volume yield from the upper tap (fig. 3.3a) would be increased in the absence of a lower tap, and this was confirmed. Not only did the single canopy taps in each tree continue to yield sap, but they did so consistently throughout the season, totalling more than the mid-bole tap the previous year (fig. 3.2a). In 1987 the canopy tap yielded sap only during two collection periods in mid-season, and then did not appear to recharge the xylem with sap to produce subsequent flow (fig. 3.1a). This is in contrast to the 1989 control, where sap flow in

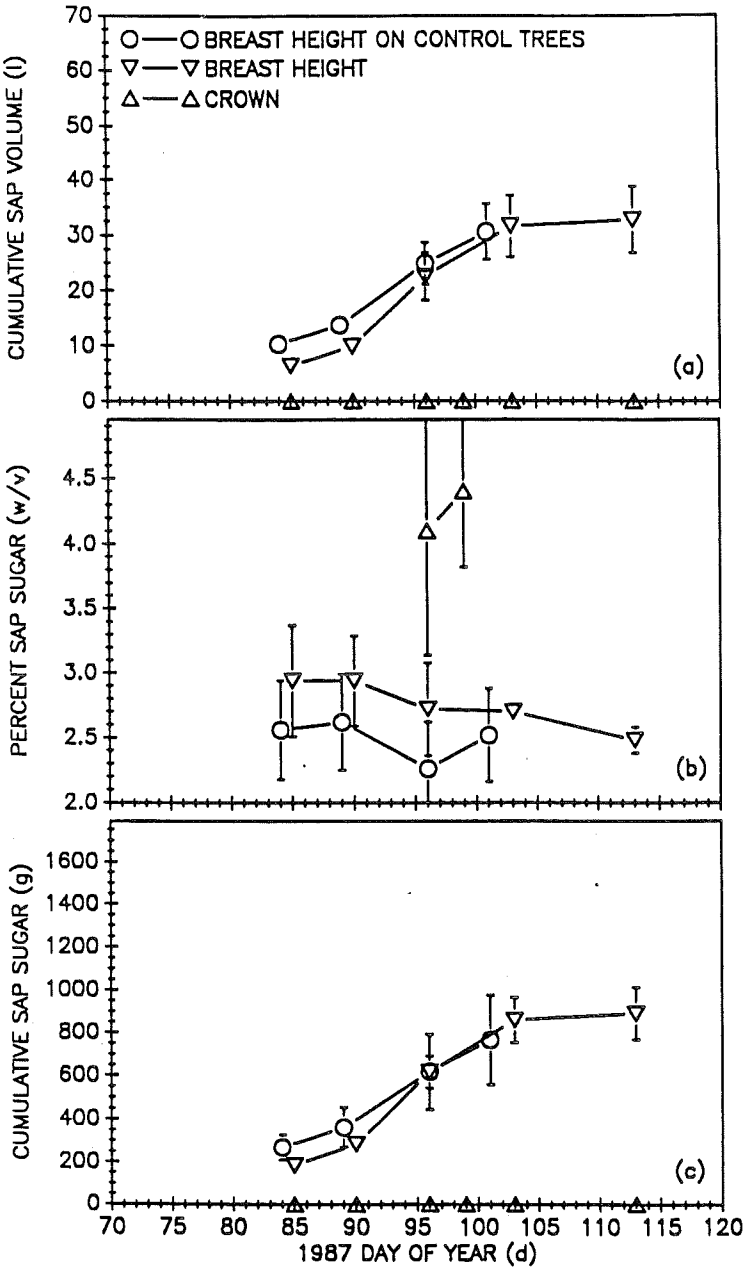


Figure 3.1 1987 results for intra-tree variation of xylem-borne sucrose production with 95% confidence interval measured from two taps per tree in five stand-grown trees (see triangles above), with crown taps at average of 13.8 m above-ground. In addition, five similar trees were selected as controls (see circles above). Crown taps yielded only very small amounts of sap (graph a), and sugar (graph c), and only during mid-season (days 96 & 99), but the percent sugar of that sap was significantly greater (graph b).

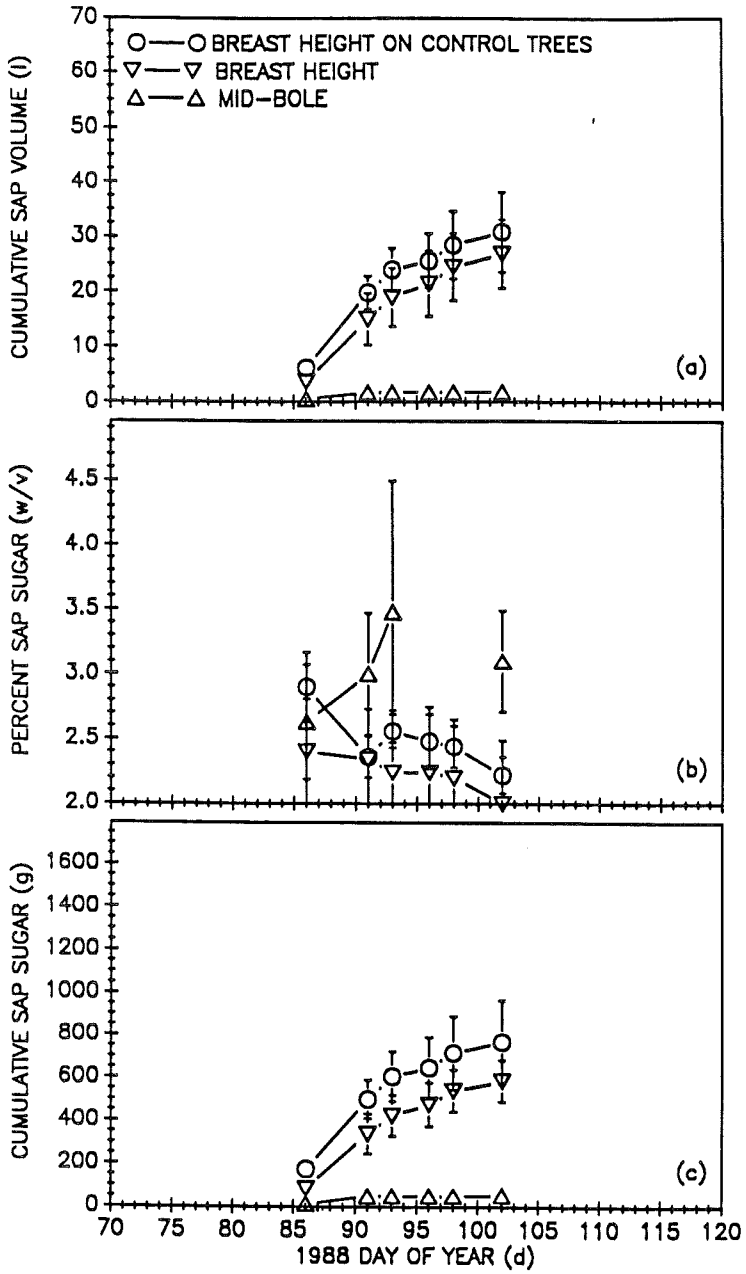


Figure 3.2 1988 results for intra-tree variation of xylem-borne sucrose production with 95% confidence interval measured from two taps per tree in five stand-grown trees (see triangles above), with mid-bole taps at average of 7.8 m above-ground. In addition, five similar trees were selected as controls (see circles above). Crown taps yielded only small amounts of sap (graph a), and sugar (graph c), and only during early-season (days 86-93) and late-season (day 102), the percent sugar of that sap (graph b), was of a greater sugar content for three of the four times measured, but only significantly so at last measurement (day 102).

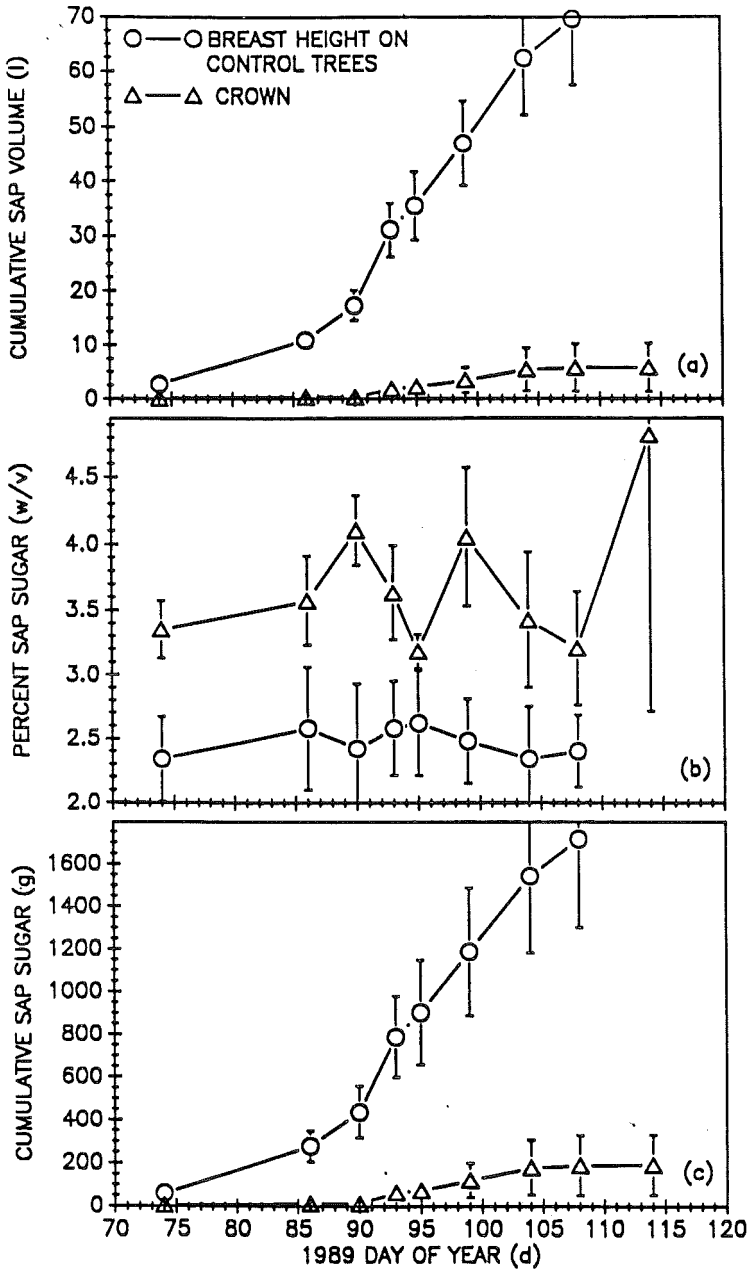


Figure 3.3 1989 results for intra-tree variation of xylem-borne sucrose production with 95% confidence interval measured from a single tap per tree in five stand- (see triangles above), at average of 13.9 m above-ground and at breast height in five similar trees selected as controls (see circles above). Crown taps yielded reduced amounts of sap (graph a), and sugar (graph c), but did so continuously through the sap season, and the percent sugar of that sap was significantly greater for the entire time (graph b).

the canopy was slow to start compared to the random trees with taps at breast height, but after the second collection period, they continued to exude sap until the end of the season (fig. 3.3a).

It is important to note, however, that while these data indicate an interaction between upper and lower taps with a negative effect on at least the volume flow of the upper tap in 1987, the effect appears to have been much less when the upper tap height was lowered and taps were closer together in 1988 (fig. 3.2a). This may have been because the taps in that year had been lowered to a level just below the limit of the hydrostatic pressure head so that the xylem in the vicinity of the top hole could be recharged by suction created by sap flow. This may not have been the case, however, because even at this lower height the tap at mid-bole yielded sap only intermittently. This intermittent yield could have been due to air entering the xylem stem at the lower tap with the negative pressure that precedes sap flow and then moving upward to embolize tissue in the vicinity of the upper tap.

The highest taps in this study were at a mean height of 13.9 m (45.25 feet) (see section 3.22), which exceeds all similar experiments. Jones et al. (1903) sampled a single open-grown tree throughout the 1901 sap season at a height of 4.7 m (14 feet), at 1.22 m (4 feet) and at ground level in a large root. Their results for sap sugar content from the upper tap contrasts with data reported

here. Based on three sap runs from the upper tap, Jones et al. (1903) reported a mean percent sugar of 2.13 percent, whereas the middle tap yielded 2.29 percent sugar or slightly higher, based on six runs, and the lowest one yielded 1.86 percent. He therefore concluded that there was no trend of increasing percent sugar with height, and that approximately breast height in all respects was the optimum tapping height. A reanalysis of his data using a t-test (Snedecor and Cochran 1980) does in fact show the upper tap to be significantly (alpha = 0.05) lower, although his methods for sugar analysis were different from those used in this study, and his results were reported to the nearest 0.01 percent as opposed to the nearest 0.1 percent.

The results reported by Jones et al. (1903) are similar to the findings of Milburn and Zimmermann (1986) for tap hole yield at 4.5 m (14.8 ft.), which was lower in percent sugar than one at 1.0 m (3.3 ft.) height for a single open-grown tree over the course of a single day. They also reported yield from two taps in the crown at a height of 8 m (26.25 ft.), for the same tree and time, one of which yielded sap and only under vacuum, but of elevated sugar content similar to the results reported here.

To eliminate any artifacts caused by vacuum sap extraction, Milburn and Zimmermann (1986) felled a frozen, stand-grown tree of approximately 10 m (32.8 ft.) height. Stem sections were placed in

plastic bags, thawed, and sugar content of exuded sap was measured. A plot of the their results for this single tree showed that below approximately 3 m (9.8 ft.) sap sugar content varied, but that above that point it rose steadily to a maximum at approximately 7 m (22.9 ft.). Above this peak, it dropped off slightly, and shoots within the crown showed nearly the full range of measured percent sugar.

In summary, these results show that intra-tree variation of sap sugar content can change inconsistently with height below approximately 5.0 m (16.4 ft.)in open-grown trees (Jones et al. 1903, Milburn and Zimmermann 1986), and among twigs in the canopy (Milburn and Zimmermann 1986). Overall, though, there is a distinct increase of sugar content with height, as when sap was measured from a frozen stand-grown tree with a wider range of sampling heights (Milburn and Zimmermann 1986) or from taps along the main stem and major branches for multiple stand-grown trees/years as was done here.

The implication of these findings is not, that tapping higher in the canopy will produce increased total sugar yields. This is because sap volume yield is greatly reduced in the crown even, as in this study, when the taps are harvested for the entire sap season (see figs. 3.1 - 3.3). These results provide a better view of functioning of the metabolic, physical, and harvest related processes which affect xylem-borne sucrose levels within the individual whole tree (see table 3.1 and fig. 3.4). This information could help to explain

Table 3.1 Production of Xylem-Borne Sucrose and Related Processes

Process	Site	Approx. Optimal Temp.	Related Reference(s)	Effect on Sucrose Pool
I) Metabolic Processes:				
Hydrolosis of Starch to Sucrose	Ray Cells	approx. 5 °C	Sauter 1967 ____ 1980	increased amount
Efflux of Sucrose to Apoplast	Contact Cells	above 5 °C	Sauter et al. 1973, ____ 1980	increased conc.
Resynthesis of Starch from Sucrose	Ray Cells	approx. 21 °C	Sauter 1982 ____ 1986	decreased amount
Initial Cell Division and Leafless Flowering	apical meristems	mean daily above 45 °C	Wyman 1950 Kozlowski 1971 Sauter 1980 ____ 1986	decreased amount
II) Physical Processes:				
Water loss via Cuticular Transpiration	branch bark	above 0 °C	Milburn & Zimmermann 1986	decreased conc.
Embolization via Cuticular Transpiration	xylem	above 0 °C	Sperry et al. 1988	increased conc.
Embolization via Sublimation of ice	xylem	below 0 °C	Sperry et al. 1988	increased conc.
Water uptake via Xylem Ice Formation	roots & upward	below 0 °C	Milburn & O'Malley 1984	decreased conc.
Positive xylem Pressure	xylem fibers	above 0 °C	O'Malley & Milburn 1983	none *
Readsorption of Sap by Embolized Xylem	upper main stem xylem	freeze-thaw cycles	herein	none
III) Harvest Related Processes:				
Sap Exudation	tap hole	above 0 °C	Tyree 1983	decreased amount
Microbial Growth	tap hole	approx. 30 °C	Ching and Mericle 1960	decreased amount

* Positive xylem pressure requires presence of sucrose (Johnson et al. 1987)

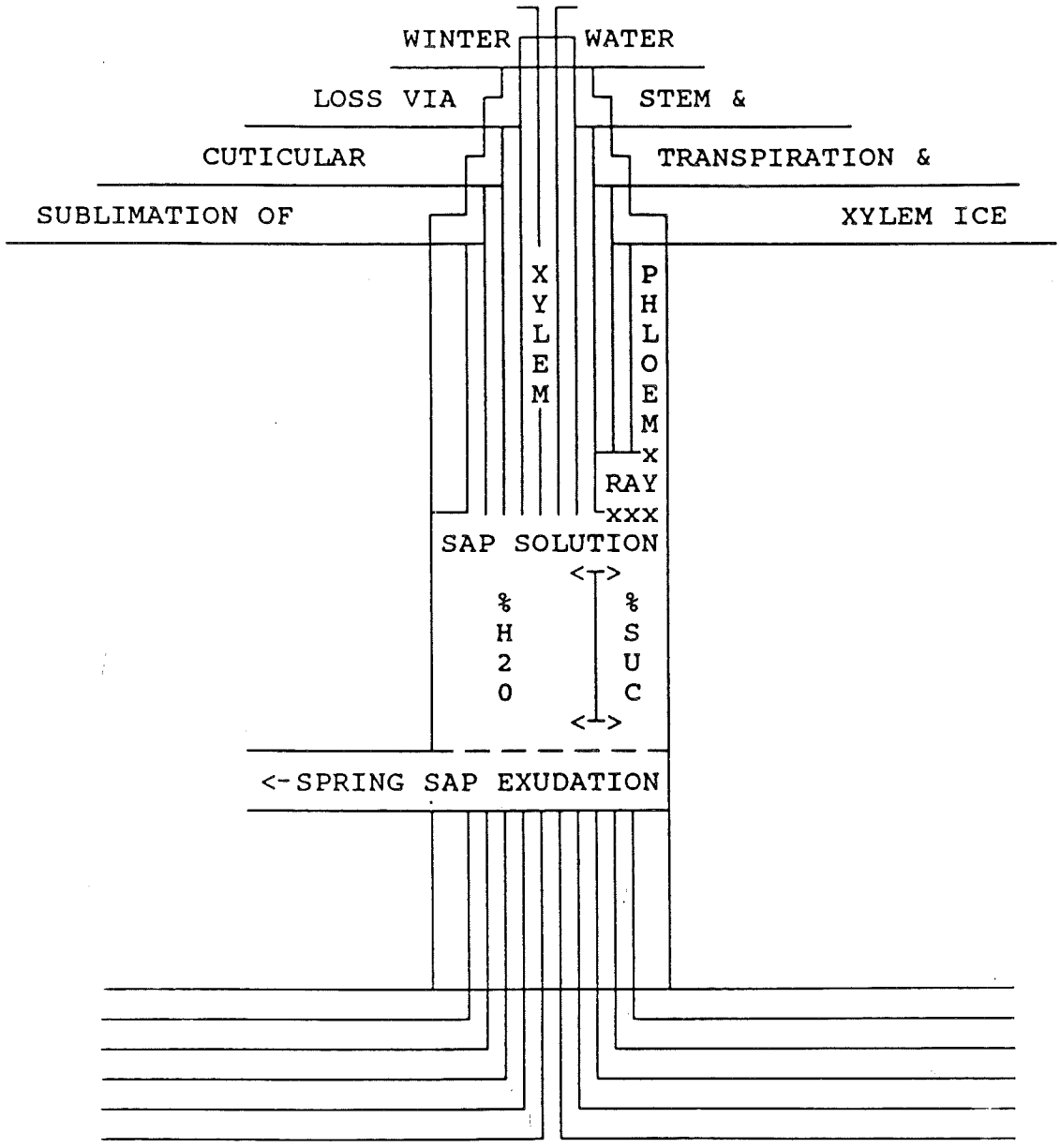


Figure 3.4 Simplified schematic of processes leading to increase in xylem-borne sucrose concentration as harvested at breast height (for details see table on preceeding page).

additional sources of spatial variation among trees, and temporal variation within and among sap seasons, if they are controlled by related mechanisms.

Perhaps one of the most important results in this study is that, although sap flow from higher taps is not as profuse as it is close to the ground, it does occur and without vacuum extraction. In addition, this flow is particularly evident later in the season or throughout the season in trees with a single tap. This indicates that the sap flow to the upper xylem, under positive xylem pressure, is acting to restore moisture to wood, which is very likely embolized; at the same time, the sap is providing a carbohydrate source to carbon sinks in the crown (see table3.1) where shoot growth must be initiated and where flowering takes place before leaf emergence.

Higher sugar concentrations of xylem sap may be more evident in the crown simply because branch surface area is higher there. This would promote increased leafless stem transpiration, as Milburn and Zimmermann (1986) estimated via potometer measurements on cut branches. The transpiration could, in turn, induce xylem embolism, not only in minor branches and in small trees as Tyree and Sperry (1988, Sperry et al. 1988) have reported, but also in the largest branches in the crown of large trees such as those that were tapped in this study. Sap exuded from taps at this level would then be more

concentrated due to the reduced moisture content of the wood and to the restricted sap flow in embolized xylem.

To test this hypothesis of sugar concentration via stem transpiration, it may be useful to compare the volume of sap flow from the crown taps (3.2 l per tree) for a 9 day period during the 1989 season (day of year 95 through day 104) to an estimate of stem transpiration during the same time. The mean diameter at the upper taps was 22.25 cm, and from the equation for mid- and upper crown leaf area in table 2.2, the leaf area above each tap should have been approximately 178.714 m^2. Estimations for sugar maple branch surface area and leaf area for the low elevation belt at Hubbard Brook Experimental Forest (Whittaker et al. 1974) can be used to convert the leaf area for the crowns at the Uihlein Station to branch surface area, which equals 57.079 m^2 per tree. This can then be converted to stem transpiration by using the stem transpiration rates observed at the Harvard Forest by Milburn and Zimmermann (1986) which, when adjusted for respective differences in saturation vapor density (Harvard Forest = 12.83 g/m^3, Uihlein Station = 4.85 g/m^3), yields a rate of 694.34 g/day. When this is then compared to the exudation rate of 355 g/day, the transpiration is almost twice as much as the exudation. As the sap moves upward via transpiration, it is not only losing water but also is also increasing in sugar content as it passes more an more ray contact cells (Milburn and Zimmermann 1986). It could also be that ray cell abundance is simply higher in the

crown xylem which would also help to account for the higher sugar concentrations observed there.

3.32 Among-Tree Variation

Of all the sources of variation in the quality and the quantity of sap production, the one that has attracted the most attention among syrup producers and researchers alike, is that which is seen from one tree to the next. This is particularly true with regard to sap sugar content, the variable that dictates the cost efficiency of evaporation and syrup production.

Variation among trees has been shown to be relatively consistent both within and among sap seasons for a given group of trees (Morrow 1952, Taylor 1956). Thus, if one could determine the cause of this variation, then appropriate silvicultural (Morrow 1981) or genetic (Gabriel 1982) manipulation could be used to control this variation and increase production, or at least to better predict production.

The consistency of inter-tree variation in the present study was measured in two groups of trees. The first was the five stand-grown trees for which there was a six year data set from 1981 to 1986, and the second was the group of seven clumped and solitary open-grown meadow trees for which there were three years of data from 1987-1989 (see Appendix D). Statistics were calculated, using a 25 percent

confidence interval and an analysis of variance for percent of sap sugar which was measured several times during each sap seasons.

The difference between individual open- and the stand-grown trees is shown by both multi-year (fig. 3.5) and yearly means (fig 3.6). The histograms in figure 3.6 are the kind of graphic display (without the confidence intervals) that Taylor (1956) first used to show the consistent tree-to-tree variation over several years. In both types of plots (figs. 3.5 and 3.6) the the open-grown trees are, clearly, less variable in sugar concentration which is also evident from the much larger f-ratio and lower p-value in the analysis of variance (table 3.2). The largest possible sample set was used for each type of tree. Hence, the open-grown trees are a slightly larger sample (seven as opposed to five), and they cover different years. Most of the difference, however, was probably because the stand-grown trees are less vigorous due to competition for light, water, and nutrients, which causes differential interaction with the climate over several years. Stand-grown individuals showed a consistent variation among trees in the percent sugar in their sap, but the consistency of the variation was far less pronounced than in open-grown trees.

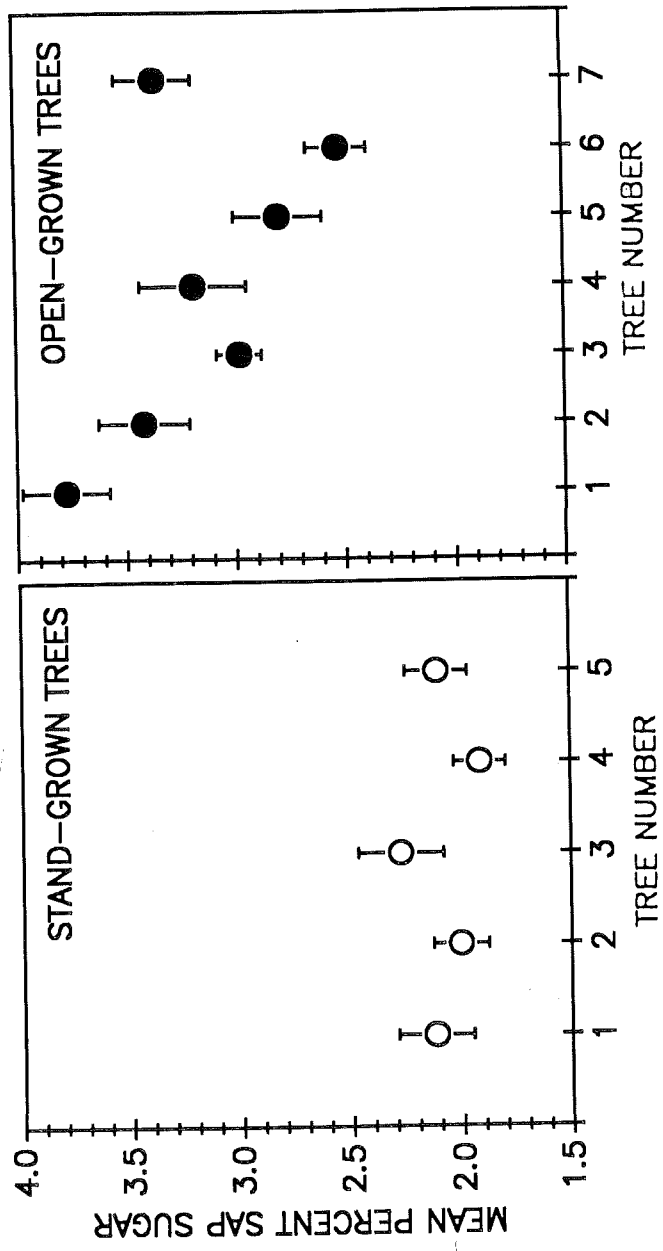


Figure 3.5 Means with 95% confidence interval for percent sap sugar for stand- (N = 33) and open-grown trees (N = 19). Percent sap sugar shows much larger range for open-grown trees and more differences among trees (for analysis of variants, see table 3.2).

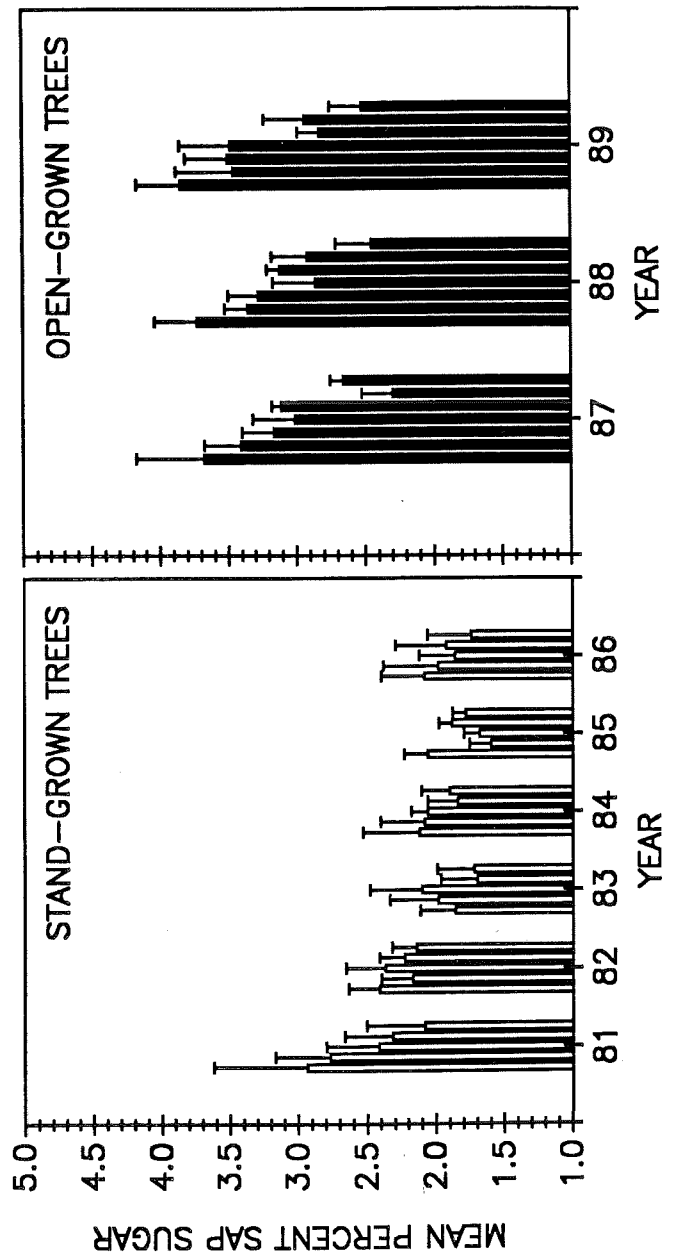


Figure 3.6 Yearly means with 95% confidence interval for percent sap sugar, for stand- and open-grown trees. Reanalysis of data in fig. 3.5, using order of bars/trees within each year from rank shown in that figure. Open-grown trees show more year-to-year consistency.

Table 3.2 Analyses of Variance for Among-Tree and Amoung-Year Variation of Sap and Sugar Production

DEPENDENT VARIABLE	FIG.	PLOT TYPE	N	SOURCE	SUM OF SQUARE	D.F.	MEAN SQUARE	F RATIO	P VALUE
PERCENT SUGAR	3.5	STAND ONLY	165	TREE	2.421	4	0.605	3.029	0.019
				ERROR	31.964	160	0.200		
PERCENT SUGAR	3.5	OPEN ONLY	133	TREE	19.920	6	3.320	19.338	0.000
				ERROR	21.632	126	0.172		
PERCENT SUGAR	3.15	STAND ONLY	165	TREE	2.257	4	0.564	4.044	0.004
				YEAR	10.453	5	2.091	14.986	0.000
				TREE * YEAR	2.679	20	0.134	0.960	0.514
				ERROR	18.832	135	0.139		

Given that consistent tree-to-tree variation in sap sugar yield does exist, it must be asked, what causes it? As early as 1903 Jones et al. hypothesized that this variation was due to the differences in leaf area of different trees. McIntyre (1932) stated that ". . . sap flow from a tree is directly proportional to its leaf area . . .". Later, Marvin et al. (1967) showed that sap volume and sap sugar content are positively correlated when production is summed over as many as 18 years. Other investigators, though, using smaller data sets, have not been able to confirm this finding (Blum 1973). The overriding interest has centered on variation of sap sugar content, and many investigators have studied this variable in relation to various crown parameters.

Open-grown trees produced higher percent sap sugar than stand-grown trees (Stevenson and Bartoo 1940), and crown class seems to be related to both sap volume and percent sugar (Moore et al. 1951). Morrow (1955) was the first to measure crown diameter and live crown ratio, as continuous variables, in order to study the influence of tree crowns on sap and sugar production. He found, using regression analysis, that these two variables accounted for only 8 to 38 percent of the variation in sap sugar concentration, depending on the sugarbush studied. Blum (1973) developed models of sap and sugar production for individual trees, based on various characteristics of crown and whole tree morphology, and these accounted for over 50 percent of the variation in multiple regressions. However, these

models were not consistent when, applied to different sugarbushes and/or different years and he concluded that the morphologic variables, including dbh, crown diameter, and live crown ratio, were not true expressions of all the causal mechanisms involved in sap and sugar production. While the variables are clearly associated, there is no direct causality. If leaf area is the controlling variable, as Jones et al. (1903) had hypothesized, then assuming that it can not be measured directly in a non-destructive manner, better variables must be found to estimate it.

Equations for estimating leaf area are species and site specific (Whitehead 1978). Work at the Uihlein Sugar Maple Station has shown that crown volume is the best predictor of individual tree leaf area for sugar maple on this site (see chapter 2). In 1988 an 1989 sap and sugar production was measured on 72 trees in the experimental plots and two solitary open-grown trees. During the intervening summer of 1988, all trees were also measure for crown volume. The two open-grown trees were beyond the range of the regression equations relating crown volume to leaf area, but were included in this analysis simply for comparative purposes.

The regression of crown volume, as an independent variable, versus the production variables of sap volume, sap sugar percent, and the sum of their product (i.e., total sugar yield) shows results (table 3.3 and fig. 3.7) that are largely consistent with those of

Table 3.3 Equations Relating Crown Volume to 1988-1989 Sap and Sugar Yield

DEP. VAR. (Y) NAME	UNITS	FIG.	PLOT TYPE	N	CONSTANT (A)	SLOPE (B)	STD. ERR. OF Y EST.	r^2
SAP VOLUME	l	3.7a1	STAND & OPEN	74	46.587	0.274	23.00	0.697
SAP SUGAR	kg	3.7a2	STAND & OPEN	74	0.591	0.010	0.630	0.798
PERCENT SUGAR	w/v	3.7a3	STAND & OPEN	74	2.010	0.002	0.330	0.299
SAP VOLUME	l	3.7a1	STAND ONLY	72	41.086	0.316	22.87	0.412
SAP SUGAR	kg	3.7a2	STAND ONLY	72	0.797	0.008	0.620	0.389
PERCENT SUGAR	w/v	3.7a3	STAND ONLY	72	2.144	0.001	0.326	0.013

N.B.: EQUATIONS FOLLOW THE FORM: $Y = A + B * X$

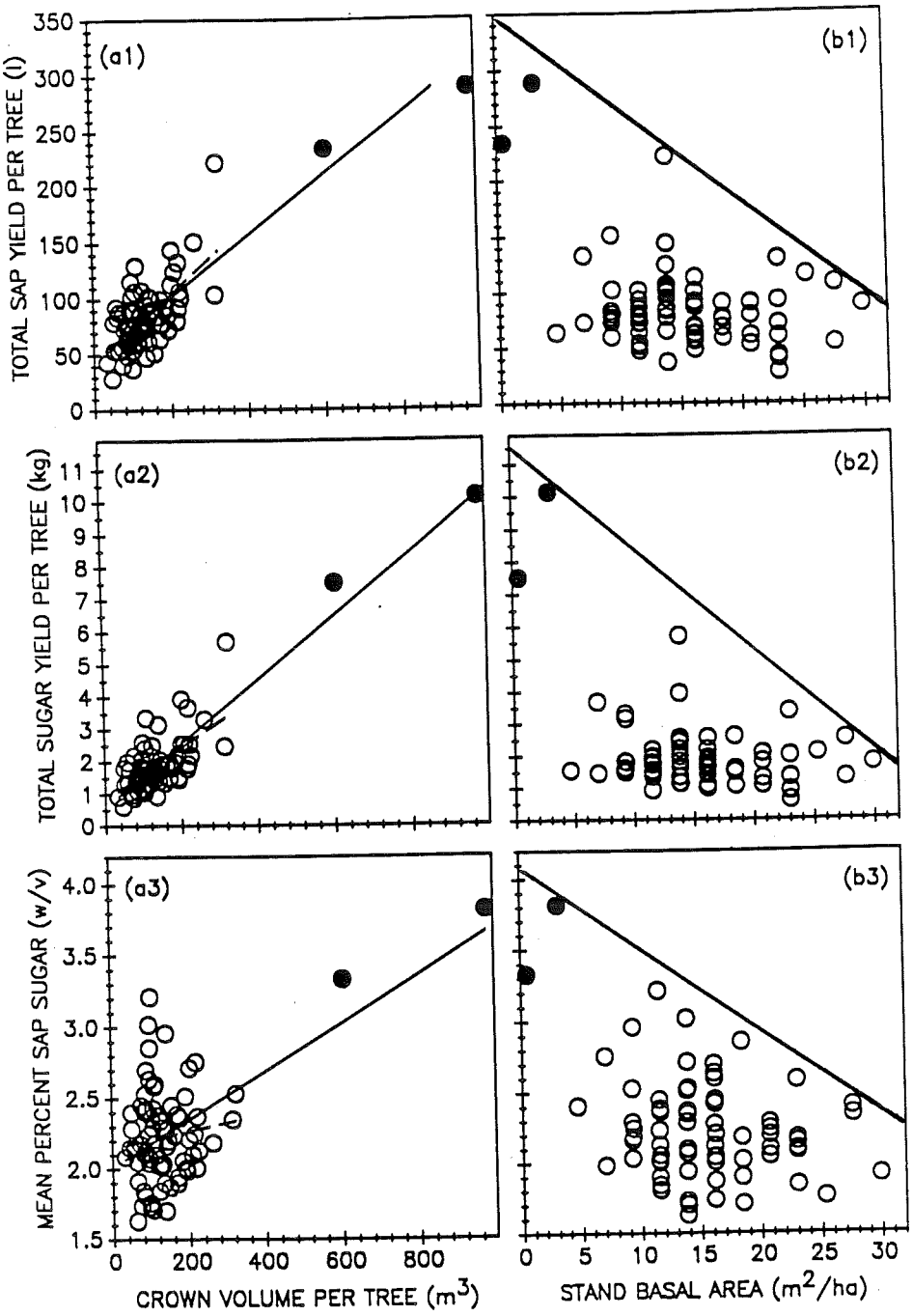


Figure 3.7 1988-1989 Total sap yield (a1 and b1), sugar yield (a2 and b2), and mean percent sugar (a3 and b3) versus crown volume (in 8/88; a1-a3) and stand basal area (in 8/88; b1-b3), for 72 stand-grown (open circles) and 2 open-grown trees (closed circles) with regression lines (a1-a3; solid line for all trees, dashed line for stand-grown trees only; for analysis see table 3.3) and boundary lines (b1-b3).

Blum (1973) and Morrow (1955) . The explanatory power of the regression models in the present study was lower than in the earlier studies, possibly because of the present results are only stand-grown trees and limited in the range of crown volume. In addition, the production of individual stand-grown trees is complicated by interaction with other trees, and therefore less consistent from year-to-year, as discussed previously.

In the final analysis, it appears that either dbh or pca (area formed by eight crown radii) is better than crown volume at accounting for variation in all three of the parameters of xylem-borne sucrose yield. This casts even more doubt on the hypothesis that leaf area is the controlling factor, because neither pca nor dbh is as effective as crown volume at predicting individual tree leaf area. Sap volume, it appears, is most closely related to pca whether or not the open-grown trees are included in the analysis (see table 3.4). For sap sugar it seems that the best association is with pca for the stand-grown trees ($r^2 = 0.461$); if the open-grown trees are included, dbh is a somewhat better predictor ($r^2 = 0.828$).

As previously discussed, it appears that intra-tree variation of sugar concentration with height is most likely to be coupled with stem transpiration as measured by Milburn and Zimmermann (1986). If this is true, and if these factors are also affecting inter-tree variation of sap and sugar yield from breast height tap holes, then

Table 3.4 Equations Relating Diameter Breast Height and Projected Crown Area To 1988-1989 Sap and Sugar Yiel Per Tree

DEP. VAR. (Y)	UNITS	INDEP. VAR. (X)	UNITS	PLOT TYPE	N	CONSTANT (A)	SLOPE (B)	STD. ERR. OF Y EST.	r^2
SAP VOLUME	l	DBH	cm	STAND & OPEN	74	-9.944	3.081	22.79	0.703
SAP SUGAR	kg	DBH	cm	STAND & OPEN	74	-1.484	0.112	0.581	0.828
PERCENT SUGAR	w/v	DBH	cm	STAND & OPEN	74	1.607	0.021	0.316	0.359
SAP VOLUME	l	DBH	cm	STAND ONLY	72	-25.727	3.615	22.87	0.413
SAP SUGAR	kg	DBH	cm	STAND ONLY	72	-1.152	0.101	0.586	0.454
PERCENT SUGAR	w/v	DBH	cm	STAND ONLY	72	1.778	0.015	0.318	0.058
SAP VOLUME	l	PCA	m^2	STAND & OPEN	74	29.337	1.683	21.291	0.741
SAP SUGAR	kg	PCA	m^2	STAND & OPEN	74	0.036	0.059	0.630	0.797
PERCENT SUGAR	w/v	PCA	m^2	STAND & OPEN	74	1.927	0.010	0.335	0.278
SAP VOLUME	l	PCA	m^2	STAND ONLY	72	30.968	1.627	21.42	0.485
SAP SUGAR	kg	PCA	m^2	STAND ONLY	72	0.530	0.042	0.582	0.461
PERCENT SUGAR	w/v	PCA	m^2	STAND ONLY	72	2.114	0.004	0.325	0.019

N.B.: ALL EQUATIONS FOLLOW THE FORM: Y = A + B * X

it may be bark or stem surface area, and not leaf area that is the controlling factor. Whittaker and Woodwell (1967) have shown that, while leaf area and bark surface area are both positively correlated to dbh, their regression lines are very different; this difference may explain why crown volume, as a proxy for leaf area, is not closely related to percent sap sugar.

In general, bark surface area relative to dbh is smaller than leaf area in small trees. However, in many deciduous trees, including sugar maple (Whittaker et al. 1974), it increases more rapidly to the point that, in some large trees, the bark surface actually exceeds leaf area (Whittaker and Woodwell 1967). This point at which bark surface exceeds leaf surface, for genotypes of varying branch morphologies, may be indicative of the potential for increased stem transpiration and sap sugar concentration with increasing size. An increased branch surface area, for a given xylem volume, should also increase the incidence of positive xylem pressure by reducing the response time for the freezing of the xylem fibers. Unfortunately, data collected in this study does not include those parameters that would allow an accurate estimate of branch and stem surface area.

For most relationships of among-tree variation, it is not a single variable which is controlling yield. A variable may, however, determine the upper limit or maximum yield. In such instances, a

boundary line analysis should be appropriate (Jarvis 1976, Webb 1972). In applying this method, it is important that there is little or no sampling error in the dependent variable. Relationships of stand density are, therefore, most appropriate because it is measured directly, either with a prism or based on the projected crown area (see section 3.3). Crown volume determinations, on the other hand, are base on the calculation that assumes that the crown conforms to a given geometric shape and will, therefore, be less appropriate.

The plots of individual tree sap and sugar yield versus stand density all show a negative slope of a linear boundary line. In all cases, the open-grown trees (denoted by a solid dot in all plots) seem consistent with the upper limit of plots of yield versus stand basal area for the stand-grown trees (see figs. 3.7b1,b2,b3).

This increase in potential percent sap and sugar yield at lower stand basal area is probably at least partially due to environmentally controlled increase in ray cell abundance with decreasing stand density (Gregory 1977). This secondary xylem tissue, and the associated contact transfer cells (Pate and Gunning 1972), has been shown to be responsible for the loading of symplastic sugars into apoplastic xylem vessels of sugar maple (Sauter et al. 1973). Morselli et al. (1978) have suggested that ray cell abundance is genetically determined and thus accounts for the consistent ranking among trees of varying sap and sugar yields as reported by

Morrow (1952) and Taylor (1956). Ray cell abundance, like other morphologic features of secondary xylem, is undoubtedly under inter-specific genetic control. Intra-specific investigations using a variety of sugar maple genetic material (P. Garrett, unpublished data) have not shown it to be significantly heritable trait (Wright 1976). What is very clear with regard to ray cell abundance is the strong degree to which it is phenotypically controlled. Gregory (1977) measured a chrono-sequence of ray cell abundance relative to other xylem tissue, and showed that its proportion increased dramatically following stand thinning. This also corresponded with increased ring width and should correspond as well with increased crown volume, pca, and dbh.

When crown volume is plotted against stand basal area (fig. 3.8a), the resultant boundary line is non-linear. This is unlike the previous plots of crown volume versus sap and sugar yield (figs. 3.7b1,b2,b3), but is reasonable because this plot most closely resembles an example of the -3/2 thinning law using the dependent variable crown volume, as a proxy for leaf area (Westoby 1977). Here there would be a linear upper limit or boundary line if a log transformation has been applied to both axes. Thus, the plot (fig. 3.8a), shows an exponential increase in potential crown volume, and therefore leaf area, with decreasing stand density, whereas the increase in sap and sugar yield is only linear (figs. 3.7b1,2,3).

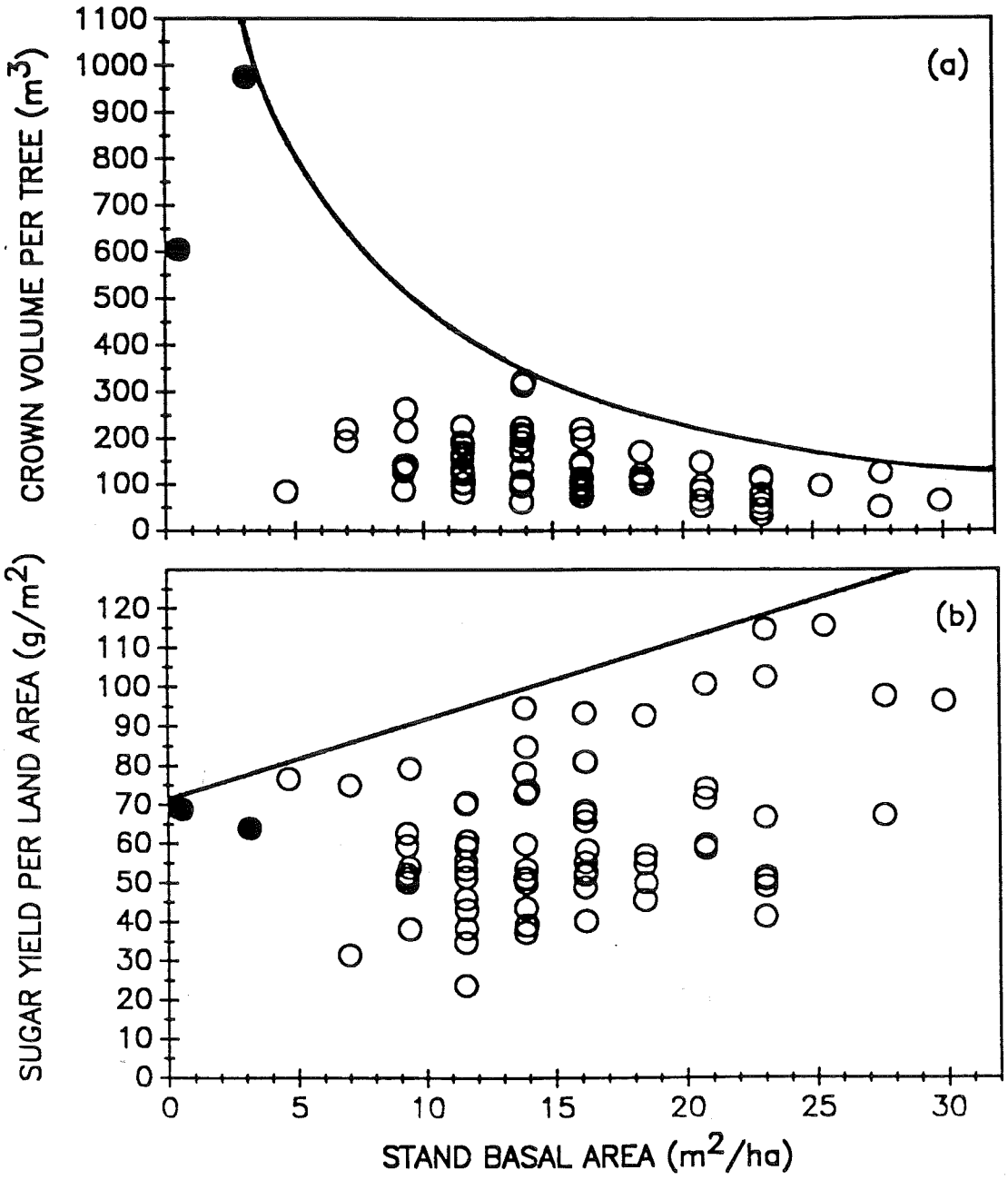


Figure 3.8 Crown volume (in 8/88; a) and 1988-1989 sugar yield per square meter pca (in 8/88; b), versus stand basal area (in 8/88), for 72 stand- (open circles) and 2 open-grown trees (closed circles) with boundary lines. Crown volume appears to conform to non-linear limit whereas sugar yield conforms to linear limit.

Sugar yield can also be estimated on the basis of pca, which represents the projected land area occupied by the individual tree canopy. A plot of crown volume against sugar yield indicates an exponential increase in potential sugar yield per square meter with decreasing crown volume (fig 3.9a,b). This is not to say that the resultant yields will be infinitely higher in small crown trees, because there are many other factors that are influence yield for closely spaced trees. It does indicate, though, that when yield is viewed on a square meter basis, the maximum yield increases with decreasing crown volume. This point is best illustrated with the stand-grown trees alone, for which the data are most complete (3.9b.).

One of the most interesting findings, relating to stand density, was a linear increase in maximum sap sugar yield per land area with increasing stand basal area (fig. 3.8b). This relationship could have important implications for management. This is because it shows that, although, open-grown trees produce more sap and sugar at, when viewed on a per square meter basis, the potential yields of individual trees are actually higher for dense stand-grown trees.

Regression analysis can also be applied to illustrate this point by using the inverse of projected crown area as a estimate of potential tree density. This can be expressed in trees per hectare

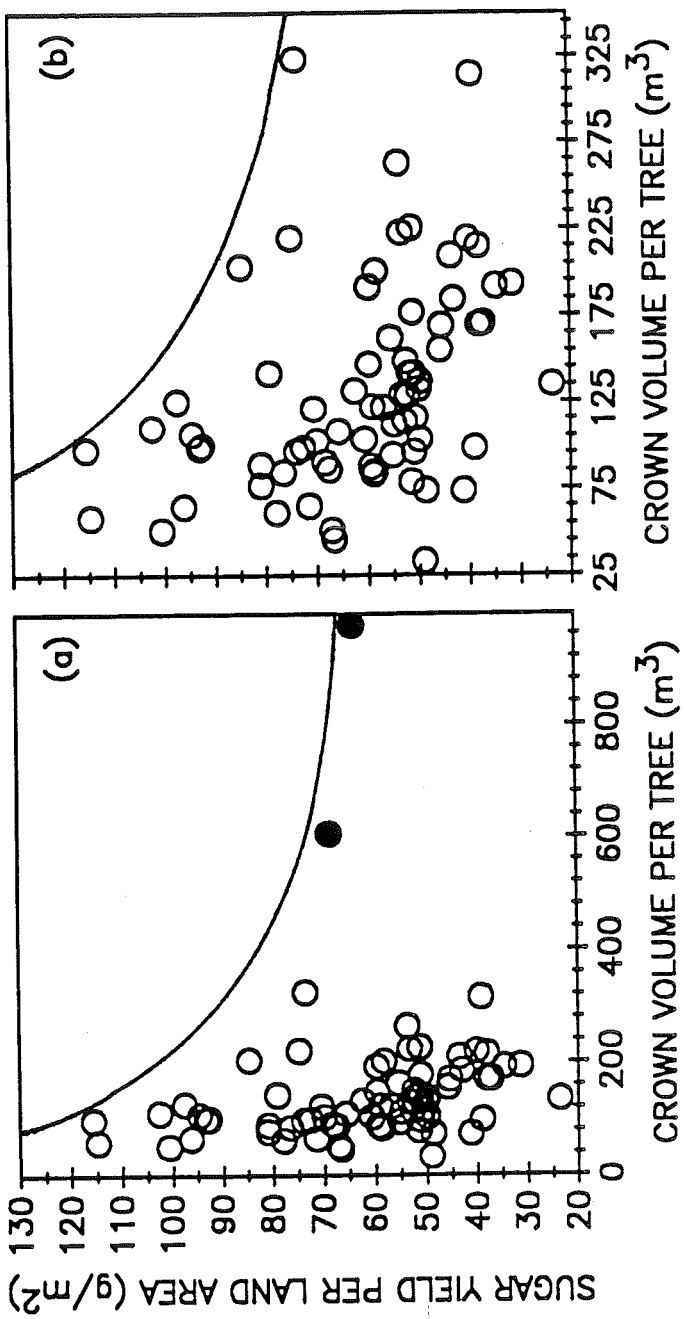


Figure 3.9 1988-1989 sugar yield per square meter pca (in 8/88) versus crown volume (in 8/88) for 72 stand- (open circles) and 2 open-grown trees (closed circles), with boundary lines. Graph a is both stand- (open circles) and open-grown trees. Graph b is stand-grown trees alone. The open-grown trees appear to conform to non-linear limit for stand-grown trees.

by assuming a stand of trees of equal size and 100 percent crown closure. A plot of the stand-grown trees on axes of density versus yield per tree reveals a relatively close relationship (r^2 = .54) as shown by a piece-wise regression (fig. 3.10a, table 3.5). The cutoff for the piece-wise regression that yields the highest r^2 value is 171 trees per hectare which is important because when the yield is converted to a per hectare basis (fig 3.10b) this is the point with the lowest yield. It is unfortunate that the data set does not include more open-grown trees to complete the range of the piece-wise regression at lower densities. By using the two open-grown trees it appears that a full range of points would yield a line with two peaks, when converted to a per hectare basis. The high points would represent optimal spacing for open-grown and stand-grown trees at approximately 120 and 600 trees per hectare respectively. The optimal density for stand-grown trees may actually be closer to 520 trees per hectare as shown by a simple linear regression of the stand-grown trees after removing two outlying data points. The outliers include a large diameter dominant tree, which in a stand setting, is probably responding more like a open-grown tree. The other is a suppressed individual with a very small crown and hence an extremely high potential tree density.

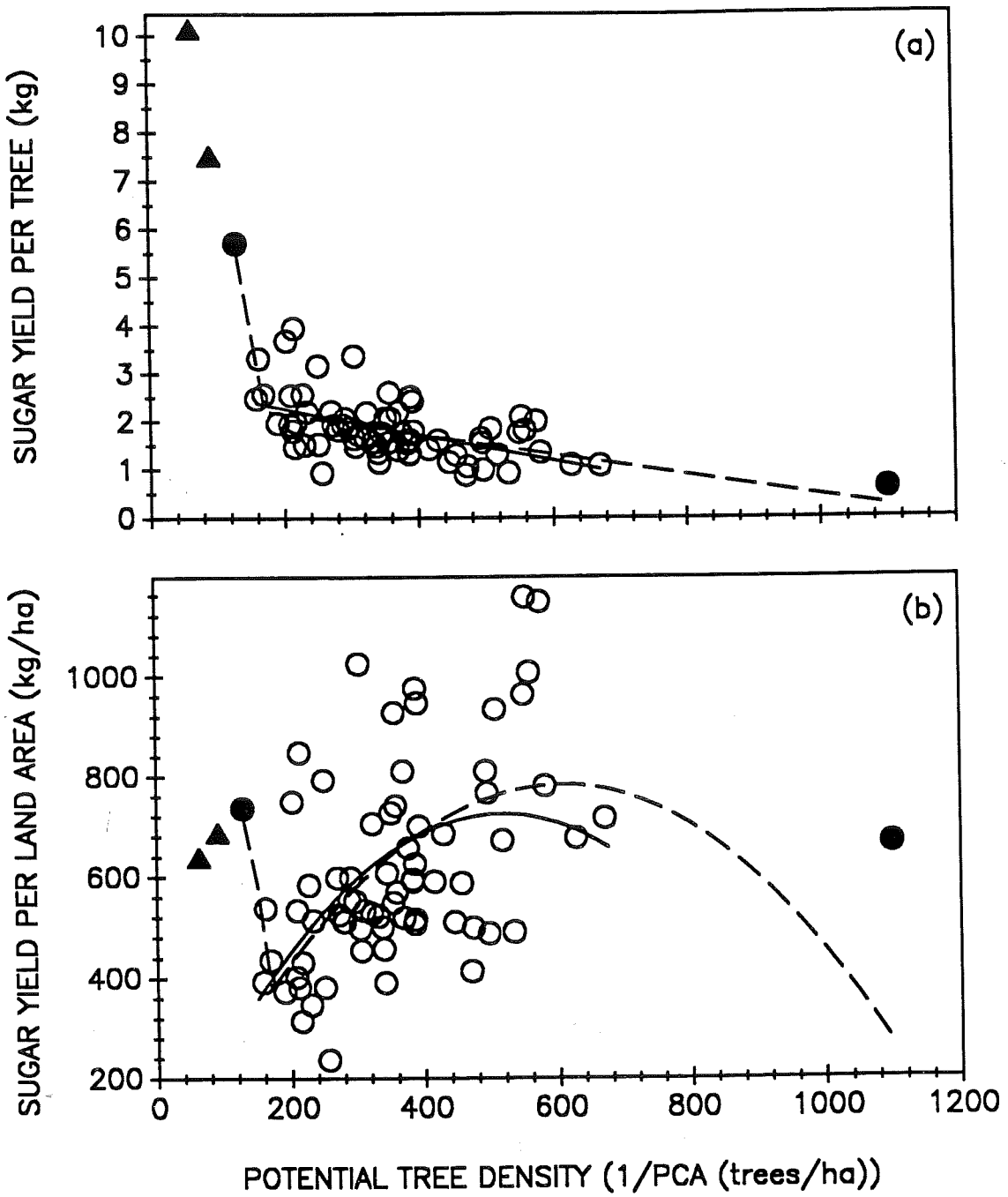


Figure 3.10 Potential tree density versus sugar yield per tree (a) with piece-wise regression (dashed-line) for all points except two open-grown trees (solid triangles). Simple linear regression performed after two outlying points (solid circles, see text) were removed. All data points and regressions convereted to per hectare basis (b) by increasing tree yield by coresponding density.

Table 3.5 Equations for Regressions Relating Potential Tree Density To 1988-1989 Sugar Yield Per Tree and Per Hectare

PLOT TYPE	DEPENDENT VARIABLE (Y) NAME	UNITS	INDEPENDENT VARIABLE (X) NAME	UNITS	N	CONSTANT (A)	SLOPE (B)	STD. ERR. OF Y EST.	r^2
PIECE-WISE X </= 171	SUGAR YIELD PER TREE	g	POTENTIAL TREE DENSITY	trees per ha	72 (*)	15872	-79.88	541.17 (*)	0.541 (*)
PIECE-WISE X > 171	SUGAR YIELD PER TREE	g	POTENTIAL TREE DENSITY	trees per ha		2575	-2.12		
OUTLIERS REMOVED	SUGAR YIELD PER TREE	g	POTENTIAL TREE DENSITY	trees ha	70	2803	-2.711	545.72	0.267

N.B.: ALL EQUATIONS FOLLOW THE FORM: Y = A + B * X
* = SINGLE VALUE FOR PIECE-WISE REGRESSION
see fig. 3.10 for plots

3.33 Within-Year Variation

Temporal variation of sap and sugar production has been observed not only during to the spring sap season, but also, to a limited degree, during the autumn when sap yield from taps is also possible. The incidence of monthly freeze-thaw conditions throughout the year creates a bimodal curve for locations at mid-latitudes (approximately 40 to 50 degrees North latitude) with peaks in the spring and the fall (Schmidlin et al. 1987). The autumn freeze-thaw events make sap harvest possible at that time, although it generally is not advisable for production purposes because sugar content is lower at that time (Knoelling et al. 1968, Knoelling 1968). At lower latitudes within the range of sugar maple (approximately 35 to 40 degrees North latitude), freeze-thaw events occur only during the winter months and sap has been traditionally harvested in winter as far south as North Carolina (Ashe 1897). The volume of springtime sap flow has been mathematically modelled and shown to be dependent mostly on temperature (Plamondon 1977, Plamondon and Berinier 1980, Kim and Leech 1985), but very little has been done to model sap sugar content.

The occurrence of a freezing exotherm followed by a thawing endotherm would appear to be important with regard to sugar maple, not only for the production of positive xylem pressure and sap exudation (Tyree 1983), but also for the elevated levels of sucrose within that sap. Gregory and Wargo (1986) sampled for xylem-borne

sugars in a single open-grown tree at 20-day intervals from October 1981 to May 1982. They found that the curve of sugar concentration with time was bimodal, with peaks in the fall and spring coinciding with daytime temperatures above freezing and nighttime lows below freezing. It may not be the actual freeze-thaw cycle, per se, which is causing the sucrose efflux to the xylem, but simply temperatures near or just above the freezing-point. Sauter and others (1973) working with sugar maple and willow (Salix spp.) (Sauter 1980) found that while the hydrolysis of starch to sucrose was most favorable at approximately 5 °C and lower, the efflux of this sugar to the apoplastic vessels was most rapid at higher temperatures.

In this study, xylem sucrose content was measured on 45 to 70 individual trees during the sap seasons of 1986 through 1989 (see figs. 3.11a to 3.14a). The sap season, or the days when sap was collected, was not identical each year and appears, in most years, to have been slightly after the peak of maximum sugar content, because in only one year (1989) was there a distinct peak of more than one data point. The date of the maximum recorded sugar content (fig. 3.11a to 3.14a) approximately coincided, however, with the date when the regression of the mean daily temperatures raises above 0 °C (see figs. 3.11c to 3.14c). During these years, on the average, the maximum recorded sap sugar was measured on day 85.25 (S.D. = 0.96) and the mean daily temperature was 0 °C on day 83.75 (S.D. = 4.78). A cubic spline curve fit (Press et al. 1986) of the mean monthly

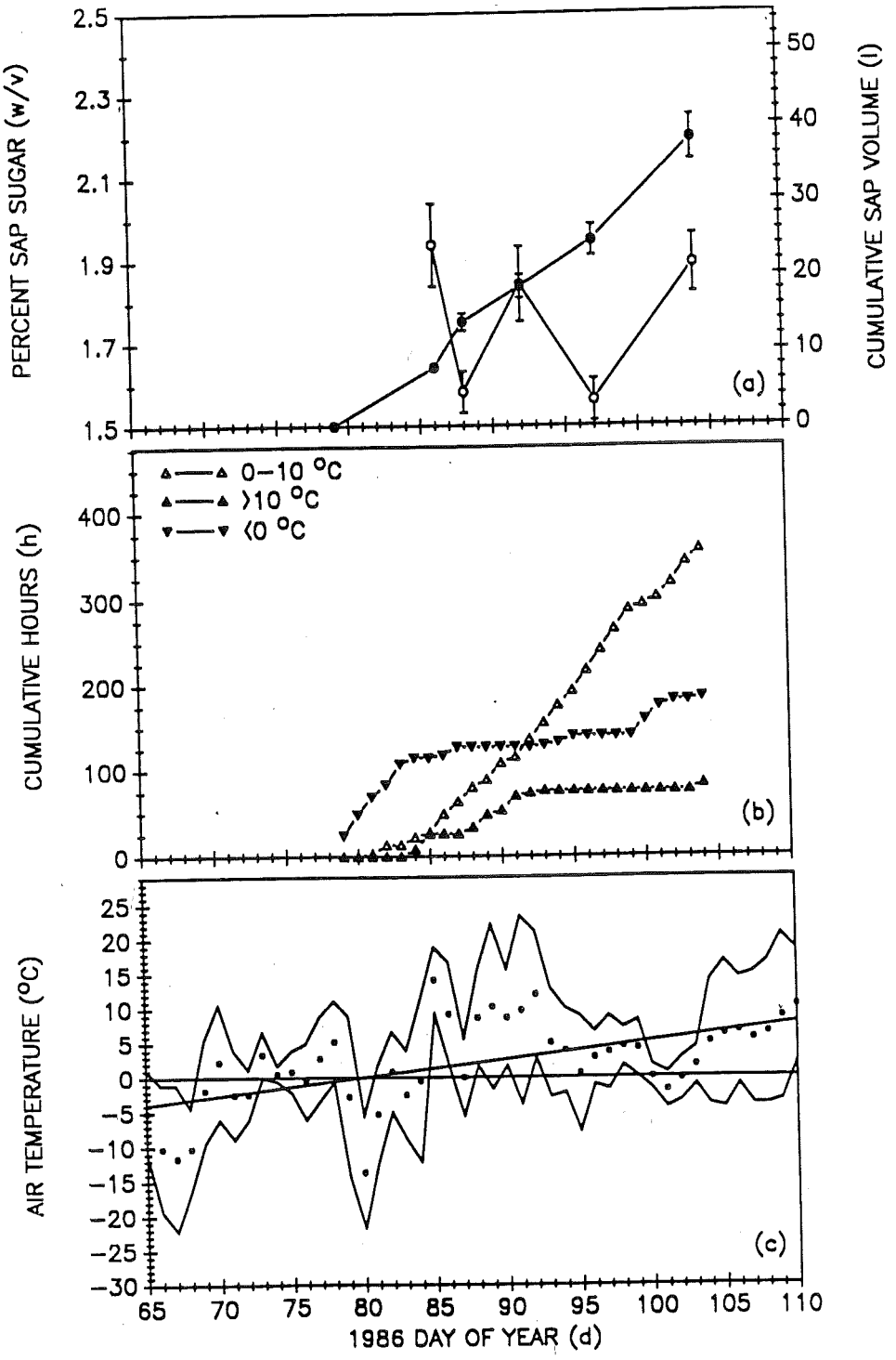


Figure 3.11 1986 sap (a; closed circles) and percent sugar (a; open circles) with hours of categorized temperature (b) and daily maximum/minimum (c) and regression of daily mean temperature (c; dots). For further details see text.

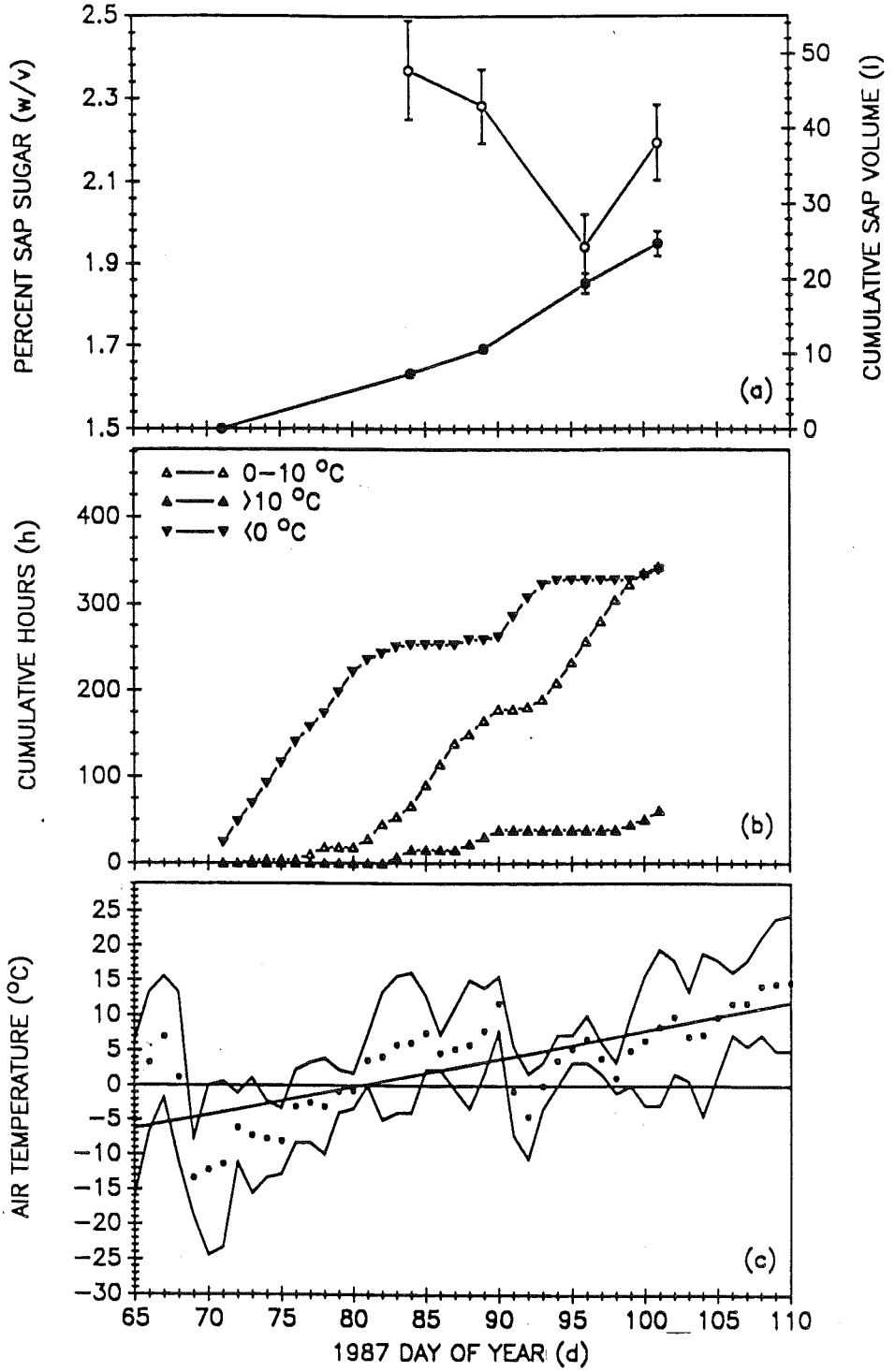


Figure 3.12 1987 sap (a; closed circles) and percent sugar (a; open circles) with hours of categorized temperature (b) and daily maximum/minimum (c) and regression of daily mean temperature (c; dots). For further details see text.

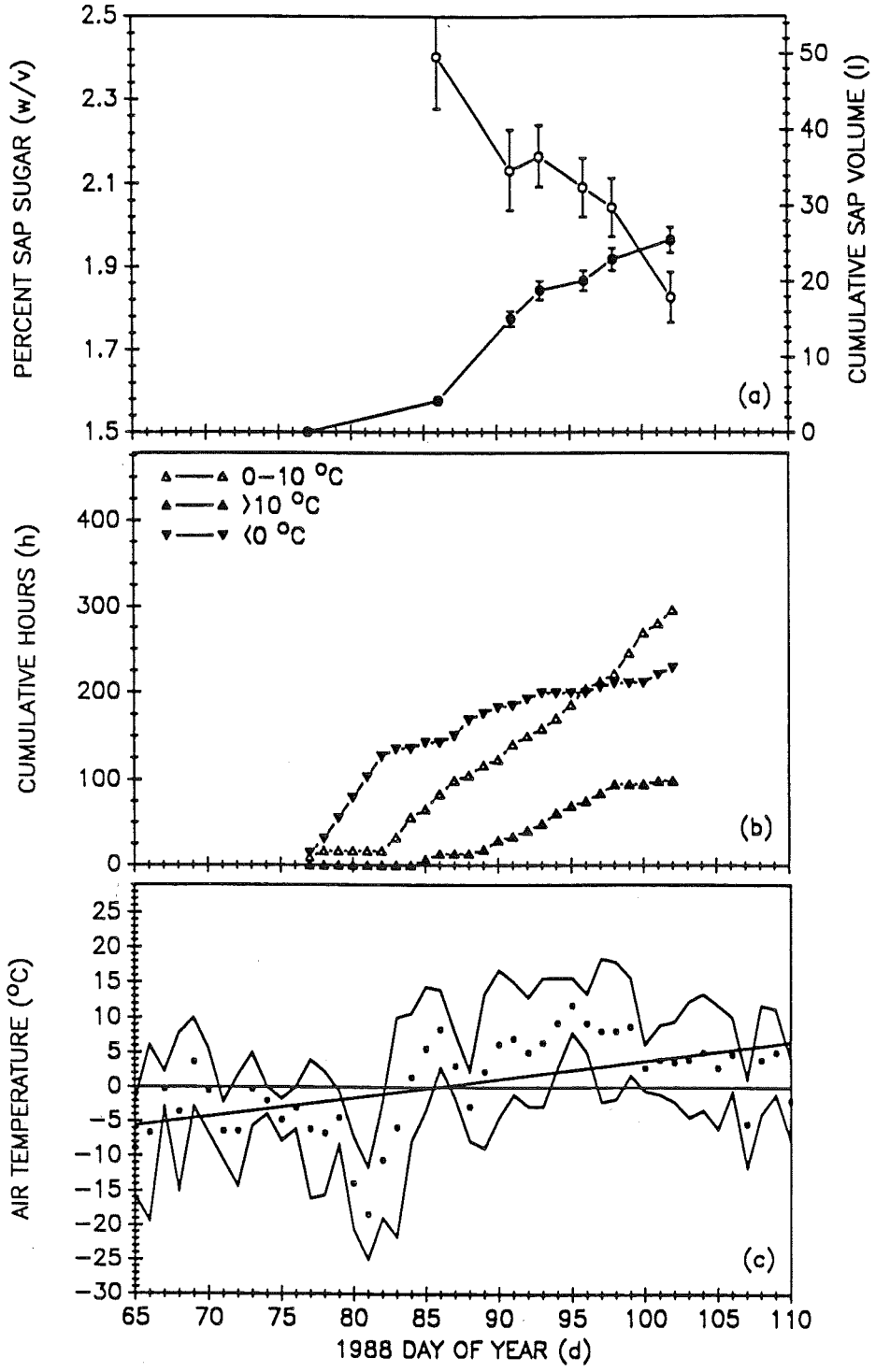


Figure 3.13 1988 sap (a; closed circles) and percent sugar (a; open circles) with hours of categorized temperature (b) and daily maximum/minimum (c) and regression of daily mean temperature (c; dots). For further details see text.

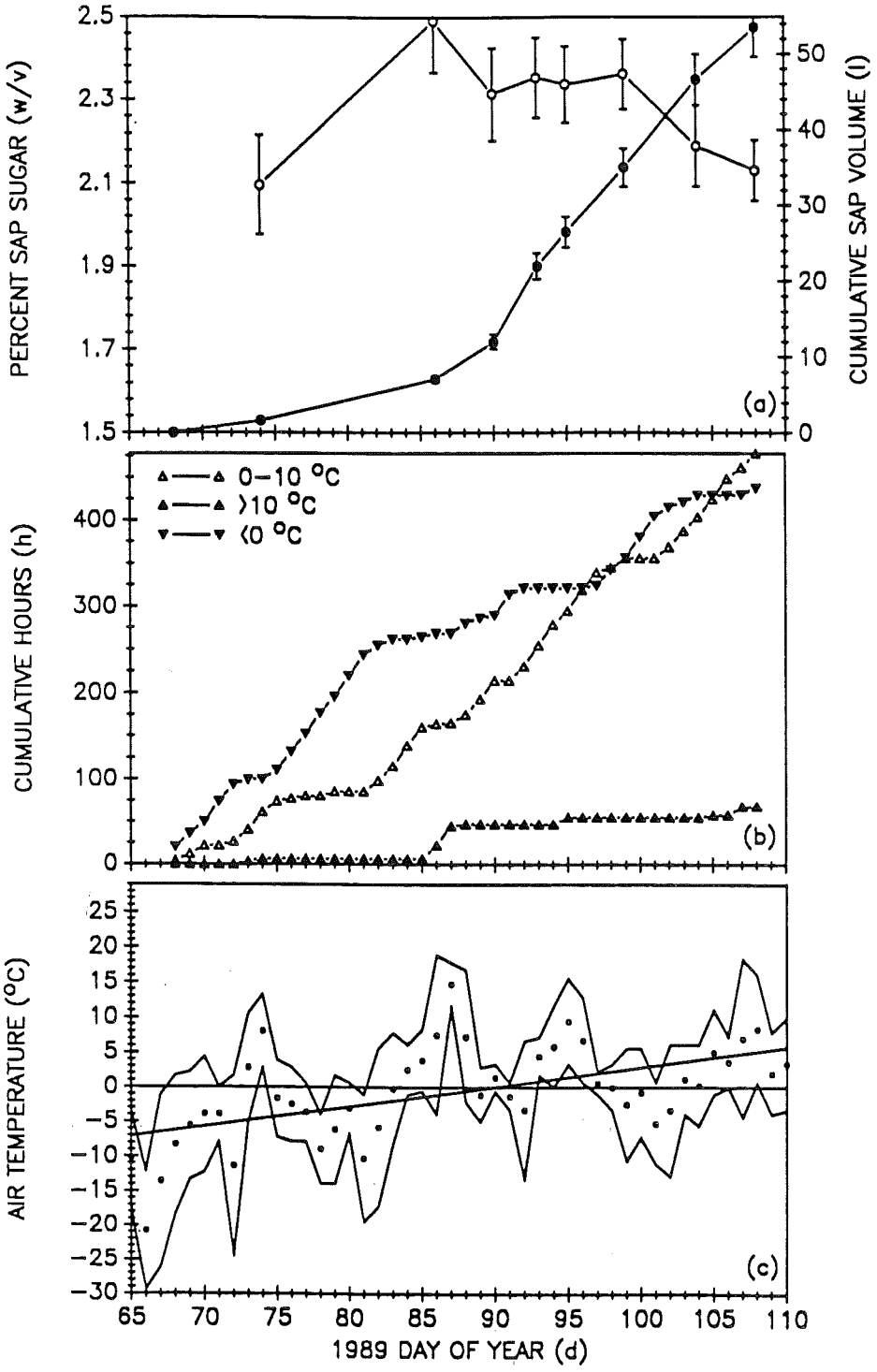


Figure 3.14 1989 sap (a; closed circles) and percent sugar (a; open circles) with hours of categorized temperature (b) and daily maximum/minimum (c) and regression of daily mean temperature (c; dots). For further details see text.

temperature over the same years passed the freezing point at 84th day of the year. A very similar date, day of the year 86, was yielded from a nonlinear regression analysis of independent sugarbush sap data from the same location collected during 1984-1989 (Appendix H). The total production and exudation of xylem-borne sucrose is dependent on the complex interaction of many physiological processes (see table 3.1). Whereas the timing of maximum sap sugar concentration coincides roughly with a mean daily temperature of 0 ^{o}C, many other factors affect the magnitude of that maximum and the rate of increase on decline on either side of it. Photosynthesis and starch accumulation during the previous growing season would seem to have the greatest impact, but defoliation experiments (Gregory and Wargo 1986) have shown starch concentrations and soluble sap sugars to be independent. Within-tree concentration of sap sugar has been shown to increase with height in the tree (see section 3.31; Milburn and Zimmermann 1986). As previously discussed, this is probably due to stem transpiration and sublimation which causes embolization of sap in inner xylem and minor branches in the canopy. The occurrence of these phenomena within a given year may also increase sugar concentration of the sap as harvested at breast height. The uptake of xylem water via roots below-ground, with freezing of stems above-ground, as presented in the model by Milburn and O'Malley (1984) would tend, in turn, to dilute sap sugars. The absolute amount of xylem sugar could also be reduced by sap exudation, resynthesis of starch from sucrose, cellular respiration and initial cell growth and

leafless flowering as the spring season progresses. Microbial growth within the tap hole (Sheneman and Costilow 1959) requires sap sugar (Ching and Mericle 1960) and also, therefore, reduces its amount. More important, though, the microbial growth dramatically decreases sap flow (Naghski and Willits 1959, Sheneman et al. 1959).

An attempt has been made to show the temperature dependence of sugar production and sap flow with the sap season (see figs. 3.11b - 3.14b). Accumulated hours at different temperatures throughout the sap season have been divided into three separate categories: a) hours below 0 °C; b) hours between 0 °C and 10 °C; and c) hours above 10 °C. Sustained decline of sap sugar concentration, and a generally low level thereafter, appears to be closely related to a large number of accumulated hours above 10 °C. This could be caused by increased loss of sugar to the resynthesis of starch, microbial activity and generally increased metabolic activity, initiating cell division and flower. These conditions were particularly evident in the years 1986 (fig. 3.11b) and 1988 (fig. 3.13b); the latter year was a mast year with increased flowering and seed production. Accumulated hours between 0 and 10 °C would tend to provide conditions favorable for the synthesis and efflux of sucrose. A balance between the middle category and hours accumulated below freezing should mean a high incidence of freeze-thaw conditions and increase flow of high sugar sap, which was particularly evident in 1989 (fig. 3.14b) when an excellent harvest of syrup was produced.

3.34 Among-Year Variation

Predicting annual variations of sap and sugar production is perhaps the greatest single challenge remaining for researchers concerned with the maple syrup industry. If this could be accomplished, it would have immense and far-reaching practical implications for the industry, similar to the implications of crop forecasting for other perennial agricultural crops such as apples. The main constraint is that it is the volume flow of sap that largely dictates the final yield of syrup (Morrow 1982). Volume flow is almost completely dependent on the occurrence of freeze-thaw cycles (Tyree 1983), and the period of time below freezing before a thaw, both of which cannot be assessed until the harvest itself is underway. Freeze-thaw conditions can be predicted spatially (Schmidlin et al. 1987), which may be useful in delimiting particular geographic regions of high potential (Tucker et al. 1989), but prediction of annual variation has not been successful.

Even if the volume of sap flow cannot be predicted, it would still be very useful if the percent sap sugar content could be, and this does show some promise. Percent sap sugar dictates the cost of the evaporation and syrup production process. Hence, if a producer knew this in advance of the sap season, profitability of the upcoming season could be assessed. As discussed previously, the photosynthesis and starch accumulation in the year preceding sap flow appears to be independent of sap sugar content. This was determined

by severely restricting carbon assimilation by repeated defoliation (Gregory and Wargo 1986). Models developed to predict yield, based on physical characteristics, have also been less than statistically significant when applied among different years (Blum 1973). Among-year variation has been most extensively studied by Morrow (1973, 1982), who examined yields of sap and sugar over a 20-year period. Morrow was unable to predict yield, but did report a negative correlation between sap volume yield and percent sap sugar. This is contrary to what has been reported on the basis of among-tree variation (Marvin et al. 1967), but is still plausible if during years of high sap flow, starch hydrolysis and sucrose synthesis from the hydrolysis of starch was not rapid enough, so that the internal sap sugar concentration was reduced.

The longest data set used in this study is for the five stand-grown trees for the period from 1981 through 1986 (fig 3.15). This is one of the data sets that was analyzed for among-tree variation (see figs 3.5 and 3.6). While there is some explanation for the consistency of among-tree variation from year-to-year (see section 3.32), one can only speculate about the cause of the overall year-to-year variation. This is a very large portion of the total variation, as indicated by an analysis of variance of the data plotted as means in figure 3.15 (Table 3.2). The F-ratio for year as source of variation is larger by a factor of ten than any other source.

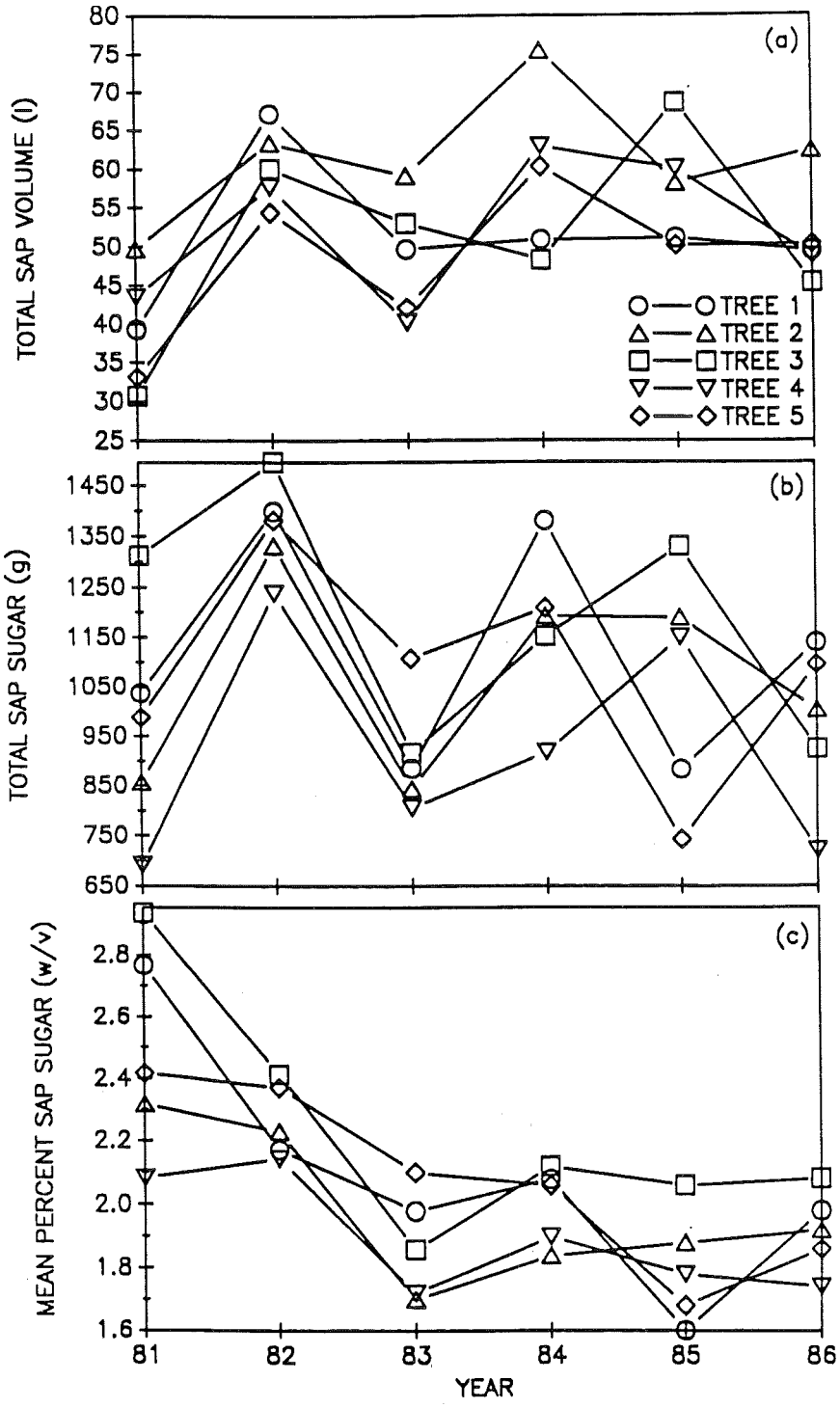


Figure 3.15 1981-1986 yearly sap yield (a), sugar yield (b), and mean percent (c), based on 5-7 measurements each sap season for five stand-grown trees (for analysis of variants, see table 3.2).

To account for this year-to-year variation it would probably be most useful to return to the explanations of within-tree, among-tree, and within-year differences. This is particularly true with regard to the hypothesis of sugar concentration via xylem embolization driven by wintertime stem transpiration. Spring sap seasons that are preceded by a high wintertime evaporative demand may, in fact, be those which show the highest concentration of sap.

It is important to note that whereas wintertime temperatures are much lower than the summer and relative humidity higher, the wind speed, in the leafless deciduous forest is considerably higher (Hicks and Chabot 1985). Perhaps most importantly, radiation loads are greatly elevated in the understory of leafless canopies. With snow on the ground, approximately 65 percent of the incident radiation is absorbed by the tree stem and branches (Federer 1972). It could, in fact, be these factors, and not growing season photosynthesis, which are having the greatest effects on xylem-borne sucrose concentration for any given year.

3.4 Summary and Conclusions

Xylem-borne sucrose production has been shown to differ between stand-grown trees and open-grown individuals. This appears to be particularly true with regard to spatial variation both within and

among trees, as opposed to temporal variation, which has always been more difficult to define. The sap sugar concentration, for example, was consistently higher in the mid-bole and canopy of stand-grown trees in this study, whereas for open-grown trees, less consistent results have been found (Jones et al. 1903, Milburn and Zimmermann 1986).

This increase in sap concentration with height may be due to the upward movement of the sap in the leafless tree driven by stem transpiration (Milburn and Zimmermann 1986), which should be highest in the canopy where absolute bark thickness is the lowest (see chapter 2) and bark surface area the highest. As the sap moves upward, it not only loses water through transpiration, but also increases its concentration by the continual efflux of sugar from ray contact cells in progressively younger and more productive xylem (Gibbs 1969). The cycles of positive xylem pressure are probably the most important force in the upward movement the sap; these cycles have has been shown by this study to yield sap, without vacuum, from even the highest taps, at an average height of 13.8 m (45.25 ft.) above the ground. This would mean that embolized xylem (Sperry et al. 1988) is being restored with moisture and mobile carbohydrates at a time when flowering and/or leaf expansion is about to begin.

The practical implications of increased sap concentration with height could be far reaching if it could help to explain other

sources of variation measured at breast height among different trees, and particularly among stand-grown trees, which have less consistent, and less pronounced, differences than their open-grown counterparts (fig. 3.5). Stem transpiration and sap concentration could be increased in genotypes with thinner bark and/or increased canopy stem surface area.

Perhaps the largest and most well documented difference between stand-grown and open-grown trees is with regard to increased potential yield per area in stand-grown trees. That is to say, the bigger a tree becomes, the less productive it is with regard to the land that it occupies. This should be no surprise, in that it seems very reasonable that an increased amount of tappable basal area per hectare should produce a corresponding increase in potential yield per hectare. This is, however, contrary to the common belief that producers should aim to develop single large crowned trees (Morrow 1955) or that sugarbushes vary only slightly in their yield per acre (McIntyre 1932). Results reported here on individual trees do not confirm these beliefs.

Practically speaking, this means that, while stand-grown trees may have lower sap sugar content, the maximum yield of syrup per hectare is much higher than for open-grown stands (fig. 3.8b). Syrup processing costs may be somewhat higher, but modern techniques such as vapor compression are being developed which reduce these costs by

as much as 80 percent or more (Kelley et al. 1989). While technologies like this do require a significant capital investment, this could be greatly offset by reduced sap collection costs over a smaller area. Sap collection has always been the most expensive and labor intensive part of any operation (Huyler 1982), and this is particularly true with open-grown trees where sap has often been collected by hand.

While spatial variation of xylem-borne sugars, particularly among trees, is generally regarded for its consistency (Morrow 1952), words such as 'unpredictability' are more often used to describe temporal variation within and among sap seasons (Morrow 1973). Within-year variation of sap flow has been modeled based on air temperature (Plamondon 1977, Plamondon and Bernier 1980), but sap sugar content has been more difficult to predict. Gregory and Wargo (1986) have pointed out that the peaks in the bimodal curve of sap concentration for a tree during an eight month period coincide with a increased incidence of freeze-thaw temperature cycles during that time.

Temperatures near or just above the freezing point may be more important than the actual freeze-thaw event for the hydrolysis of starch and the efflux of xylem sugar (see table 3.1). The day of the year on which the regression of the mean daily temperature raises above freezing point has been shown in this study also to coincide

well with the maximum recorded mean sugar concentration for many trees during the years 1986-1989. If this relation applies over many years for individual trees, and for whole stand yields for sugarbushes, then it may have some practical implications for syrup producers. The day during the spring when the mean daily temperature passes above zero could be seen as the optimal center of the sap season for a given region or climatic zone. Centered around this date should be the period with the highest incidence of both the freeze-thaw conditions that produce sap exudation, and a temperature regime favorable for the production of xylem-borne sucrose.

While a mean daily temperature of zero, or just above, may indicate the seasonal high point in sugar concentration, variation on either side of that peak is far more difficult to explain. This situation is largely due to the multiple sources of interacting variation which impact xylem sucrose production over the course of the sap season (see table 3.1). A modest attempt has been made to model these fluctuations based on accumulated hours at particular temperature categories (table 3.1 and figs. 3.11b to 3.14b), but additional efforts will be necessary to account more fully for the variation.

The temporal variation of sap and sugar production, and the prediction of yield among seasons, illustrates the great challenges still facing researchers concerned with the maple syrup industry.

Little progress has been made in this area to date and a reexamination of previous assumptions is called for now. It is becoming increasingly clear that leaf area and photosynthetic production of starch, as a precursor to sucrose, may be far less important than previously believed.

In the future, it is expected that more fruitful results could be obtained by carefully examining the mechanisms within a tree that affect overall sugar concentration, and in particular, factors such as wintertime stem transpiration, whose potential could vary widely from tree to tree, and from sap season to sap season. The effect of wintertime evaporative demand on the leafless forest is rarely considered, but it could very well be this demand, not growing season photosynthesis, that most impacts springtime sucrose levels.

Chapter 4: Future Research:
Conclusion to the Dissertation

This dissertation has focused on the phenotypic variation of foliar morphology and xylem sucrose production in individual sugar maple trees. In the final analysis, it does not appear that foliar morphology in general, and leaf area in particular, are directly linked to sap quality or sugar concentration. Leaf area, on the other hand, does appear to be very closely related to overall tree growth (see Chapter 2) and the total amount of xylem-borne sucrose produced over a given period of time, particularly with regard to stand density and the yield of sugar per unit land area. What may be much more important with regard sap concentration is the area of the leafless shoot cuticle on primary tissue and stem bark through which wintertime transpiration occurs, hence, removing water and concentrating the remaining xylem sap. Stem surface varies differently from leaf area (Whittaker and Woodwell 1967) and was not foreseen as an important parameter when this research was undertaken. Like many research projects, this one has answered several pertinent questions, but has also posed many for future investigation.

Based on the results and conclusions presented here, research could proceed with further studies. Such work should include additional levels of pursuit such as investigating the genotypic

variation and scaling-up individual tree results to the stand and regional levels. Parameters other than foliar morphology should also be examined on the phenotypic level, such as wintertime evaporative demand and stem transpiration, to better define the mechanisms within the individual tree. What follows is a list of six broad areas of research, listed in order of priority. In several of these areas, particularly the first two, considerable research is already underway at the Uihlein Station.

1) Results of individual tree yield versus density, based on point density and projected crown area measurements, should be scaled-up to the stand level with existing experiment station data. These findings could be extended to on-farm research with cooperating syrup producers to determine the overall economics of production, using varying sugarbush densities and syrup concentration technologies.

2) Genetic variation of foliar morphology needs to be assessed based on existing data, and pursued in conjunction with measurements of xylem sucrose content and photosynthetic efficiency. In light of results reported here, it may also be useful to examine the heritability of bark thickness and the potential wintertime evaporative demand of different crown morphologies, particularly with regard to commercial varieties of sugar maple with identified and consistent crown

morphologies.

3) Phenotypic variation of wintertime stem transpiration should be modeled for the individual tree. This should first be done based on weather records and records of sap and sugar yield over different years because among-year variation is clearly the largest. The investigations could move to differences among different trees to develop a particular ideotype. In both of these efforts, heat pulse velocity studies may be useful for measuring sap movement in response to stem transpiration.

4) Efforts should be made to develop a mathematical model for within-year variation of xylem-borne sucrose concentration as affected by ambient temperature. This would be based on the results from #3 above and additional parameters from table 3.1. An initial effort would use published results of the rates of starch hydrolysis, efflux of xylem sucrose, microbial consumption of sucrose, etc. and additional data collection as necessary.

5) Chrono-sequences of xylem morphology should be developed, particularly with regard to within-tree xylem accumulation at varying heights in the 18 trees studied in chapter 2, and ray cell abundance of thinning plot trees which were measured for sap and sugar yields and reported in chapter 3. Xylem age for a given amount of projected crown area should be a good indication

of crown bark surface area and stem transpiration. Ray cell abundance has been traditionally thought to dictate sap sugar content, but has not yet been measured on trees at the Uihlein Station.

6) If necessary, whole-tree morphology can be reassessed in ongoing efforts to develop an ideotype for syrup-producing sugar maple. This should include accurate estimations of bark surface area and a more detailed assessment of crown volume as an estimator of leaf area using the height of each radii instead of a single height to maximum diameter of the crown.

This list is only a sampling of the possible research related to the production of maple sap and syrup. In 1903, C.H. Jones made the point that, "Although it is an old-time industry, neither sugar-making nor the tree from which the sweet sap flows have hitherto received the close scientific study they merit." This statement is as true today as it was then, particularly with regard to the biology of sugar maple.

APPENDICES

APPENDIX A:

CRITICAL CHARACTERISTICS OF NEW YORK STATE MAPLE SYRUP PRODUCERS: SOCIO-ECONOMICS, TRADITION, AND PERSONAL EXPERTISE[1]

INTRODUCTION

The basic question examined in this study was: to what extent do socio-economics, tradition, and personal expertise affect decision-making by New York state maple syrup producers and how can this information aid research and extension professionals concerned with the industry? Our original intention was simply to use the results for our own information, but after an overwhelming demand, particularly from those answering our questionnaire, we decided to expand the study and to report on its results.

METHODS

Information was collected by an identical written questionnaire that was presented, with an explanatory cover

1 Adapted from a series of two articles (Tucker and Tucker 1989a,b)

letter, to all participants in the New York State Maple Tour from 1986 to 1988. Over the three years, 75 different families responded, from 29 of the 60 New York Counties, and five from nearby states. Results for each question were tabulated and are presented here as a percent of the total number of respondents.

RESULTS AND DISCUSSION

Socio-economics and Tradition

The largest part of the questionnaire asked questions about the socio-economics of maple syrup production and where maple production fits into the overall functioning of the farm or family unit. The number of years that participating families had been involved in the production of maple syrup ranged from 1 to 137 with an average of 45 years. Producers had an average of 2550 taps with a range from 315 to 10,000 taps.

The question, "Why do you produce maple syrup?" produced the most interesting answers and some of the funniest as well. Respondents were asked to list several reasons. Responses included 57 percent who listed profit as a motive, 52 percent who thought it was pleasurable, fun, challenging or interesting and 19 percent who said they did it as a hobby. It is also important to note that 27 percent listed tradition and family as reasons. Several said, "it's in my blood" and one said "it's in my damn blood!" Also, 19 percent listed the product as a reason and one person said, "because my wife

collects saps!"

In the next question, respondents listed their farm activities and ranked the importance of each to their farm's economy (#1 being the most important). Most farms showed a variety of activities, with sugaring consistently ranking about second in importance to overall farm economy (average rank for maple came out to 1.8). Altogether 35 percent listed dairying as an activity, and it was generally ranked #1 in importance to the farm economy. Other activities included: sawmill, firewood, vegetable garden, row crops, custom combining, beef, honey, timber, maple equipment sales, dairy replacements, Christmas trees and renting out land.

These data clearly support the idea that syrup production is often an important secondary source of income that is frequently used as part of a diverse scheme to maximize overall farm output. Also supported is the notion that sugaring and dairying often go together and complement each other. Probably, several reasons are responsible for this coexistence of farm operations including: the spring sugar season, compared to the fall harvest, is a relatively quiet time when the cows are still in the barn; the spring sugaring can supplement cash flow for the farm at a time when money is often badly needed to purchase seed and fertilizer and otherwise begin planting; and vacuum tubing technology for harvesting sap is not unlike vacuum powered milking machines.

In answer to the question, "Do you use maple to offset losses in other farm enterprises", 27 percent said that maple sugaring did in fact help to make up for losses elsewhere on the farm. It would be interesting to know how many farmers who participated in the dairy buy-out program in turn increased their production of maple syrup. While we did not find that out, it is significant that many families do use maple to offset losses in other farm enterprises. Clearly most farmers do not need sugaring to fill this role, but in these times when many small family farms are struggling to be economically competitive, it is important to note that syrup production can, for many families, make the difference.

In the last question we asked, "who participates in maple production on your farm?" Maple syrup production is definitely a family affair, according to the answers we received. Of those who responded, 78 percent said that their spouses were also involved, 68 percent indicated children, 16 percent said parents and 41 percent responded that other relatives participated. The last two categories of participants in the question were friends and hired labor which were each indicated by only 35 percent of the respondents.

Personal expertise

The first question asked concerning sugarbush management was, "Are there any signs which you look for in a sugar maple tree which tell you whether it will produce a high sugar sap?". While 50 percent of the respondents stated that they looked for a large crown, 33 percent said they looked for healthy vigorous growth. In addition, three respondents said they looked for trees with many limbs, and two said that stressed trees might produce a high sugar sap. In a related question about large quantities of sap 53 percent of the respondents said they looked for large crowns, 19 percent looked for healthy, vigorous growth, 5 percent looked for a moist site and 4 percent mentioned "many limbs".

The next question asked, "Are there any signs which tell you what area will make a good sugarbush?" While some people gave answers about the accessibility for tapping, the majority gave answers related to the ecology of the woods. The largest number of responses were concerned with the orientation of the slope. Most respondents thought southeastern slopes offered the best sugarbush areas; a few mentioned south and southwest aspects as well, and one person said a south or southeast slope should not be chosen because although the run starts earlier it also ends earlier. These answers could give rise to some interesting experiments, assuming other sources of variation could be controlled.

Soil fertility was important for 25 percent of the respondents to this question. Some were more specific and said what kind of soil was good for a sugarbush but there was some disagreement between answers. Some said loamy soils were good, others said heavy soils, others said soils that soils that were not heavy were preferable. This is another area where it is clear that the producers have done some observation or even informal experimentation on their own lands.

Some of the most interesting answers to us were three descriptions of the other species likely to be present in a good sugarbush, such as beech, hop hornbeam, or ash and birch. As two other respondents stated, "ground cover types are indicators of soil fertility." This is interesting because the method of judging the productivity of forest land based on the plant types growing there has been used by other farmers and foresters concerned with tree growth all over the world, but it is rare to hear of indicator species being used to help determine sugarbush production.

CONCLUSIONS

It is difficult to say how representative these results are for maple syrup producers as a whole or even those in New York State alone. Participants in the yearly maple tour are in many ways a very special group of people. Certain characteristics indicated by the responses, however, clearly stand out as being critical to New York maple syrup producers in general and most likely to others in the

northeastern U.S. as well. Not only did the majority of those responding say that financial profit was a major incentive, but many also said it was pleasurable. This is an important combination that is not always found in all industries.

Another critical characteristic appears to be the role that tradition and family play in syrup production. Over one quarter cited tradition as an important factor in their decision to be involved in maple production; perhaps most important was the overwhelming indication that maple syrup production is so clearly a family affair. It is also quite clear that maple producers as a group think a great deal about the ecology of their sugarbushes and generate hypotheses about what will increase production, as well as making observations about the morphology of individual trees in relation to their sap and sugar production.

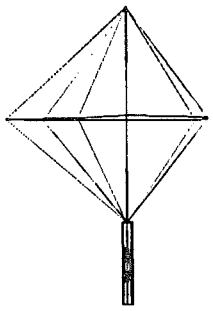
For us as researchers, the most important outcome of this study is not the results themselves but the ideas or hypothesizes that they generate for future work. Maple syrup producers, other farmers, and landowners in general are an important source of information. They have much to offer to researchers who are willing to work closely with them to improve maple syrup production and the industry as a whole.

APPENDIX B: Table B.1 Summary of 18 Sample Trees

TREE No.- ORDER CUT	STAND B.A.- TAPE (ft/ ac)	STAND B.A.- PRISM (ft/ ac)	STAND STEMS PER ACRE (>2")	STAND MEAN DBH (in)	STAND HIS- TORY	TAP HIS- TORY	CROWN CLASS	DIA. CLASS (in)	PRE DBH (in)	POST DBH (in)	PRE HT (ft)	POST HT (ft)	PRE HCB (ft)	POST HCB (ft)
1	92.42	80	110.9	11.42	THIN	TAP	CD	14-15.99	14.6	13.77	74	75.45	42	42.65
2	74.18	100	88.73	11.7	THIN	TAP	CD	12-13.99	13	12.28	79	76.11	47	48.55
3	49.06	80	199.6	5.677	UN	UN	UND	4-5.99	4.8	4.363	54.5	54.46	30.5	30.51
4	55.63	90	199.6	6.588	THIN	UN	INT	6-7.99	7.5	6.927	68	68.89	20	24.60
5	100.45	80	133.1	9.316	THIN	UN	CD	8-9.99	8.15	7.753	69	70.86	41	41.99
6	116.17	90	266.2	7.366	UN	UN	CD	10-11.99	10.6	10.35	70	69.88	28	30.51
7	78.51	70	199.6	6.977	UN	UN	INT	6-7.99	7.2	6.612	71.5	70.53	45.5	48.55
8	77.55	100	288.3	6.453	UN	UN	CD	8-9.99	9.3	8.186	77.2	76.11	42.2	36.74
9	76.30	90	110.9	11.16	UN	UN	CD	12-13.99	13.4	12.39	78	68.89	37	40.68
10	59.20	60	266.2	4.133	THIN	UN	UND	2-3.99	2.8	2.489	29	29.85	4.7	4.593
11	36.44	40	421.4	3.357	THIN	UN	UND	0-1.99	1.7	1.375	16.7	17.06	1.8	1.640
12	139.39	90	266.2	8.708	UN	UN	DOM	14-15.99	14.4	13.53	80	78.08	26	28.87
13	127.60	70	221.8	9.41	UN	UN	DOM	16-17.99	16	15.11	80.8	71.85	32.8	33.89
14	84.79	80	199.6	7.677	THIN	UN	INT	4-5.99	5.6	5.274	39.7	47.90	5.4	4.921
15	122.66	110	399.3	6.272	UN	UN	UND	2-3.99	2.9	2.705	41.3	41.33	4.5	3.937
16	147.88	100	288.3	8.084	THIN*	TAP*	DOM	16-17.99	17.1	16.24	80	65.94	22	21.65
17	129.33	120	354.9	7.306	THIN*	TAP	INT	10-11.99	11.5	10.51	74.7	66.60	44.7	42.65
18	96.63	100	732	3.548	UN	UN	UND	0-1.99	1.3	1.221	23	22.96	5	4.593
MEAN	86.702	83.333	229.2	7.731	THINNED			MEAN	8.991	8.396	61.46	59.60	26.67	27.30
MEAN	98.208	88.888	298.2	7.286	UNTHINNED			S.D.	4.961	4.722	21.03	18.90	15.84	16.16
S.D.	33.648	22.110	106.6	2.698	THINNED									
S.D.	28.268	12.862	170.2	2.106	UNTHINNED									

N.B. * = self-thinning or tapped historically but not in recent past
POST DBH = diameter breast height measured dried disks removed after felling
POST HT = Tree height measured as the total length of felled tree
POST HCB = Height to crown base measured on felled tree

Figure B.1 Three-dimensional computer drawings of the 18 sample trees oriented with the magnetic north radii into the page.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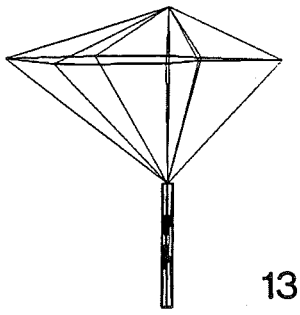
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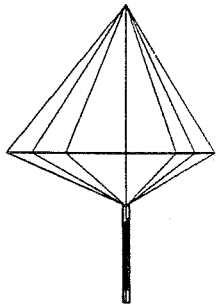
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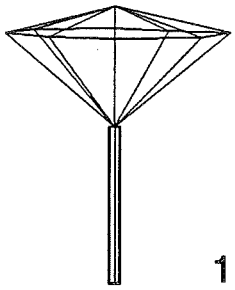
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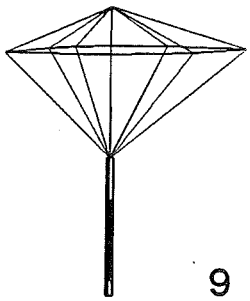
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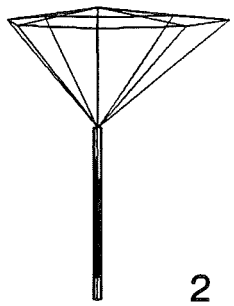
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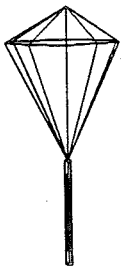
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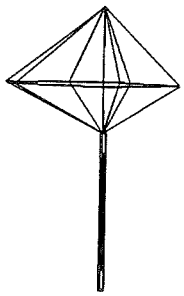
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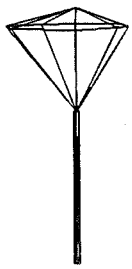
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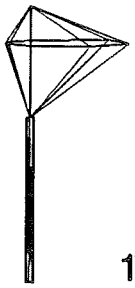
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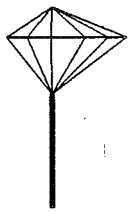
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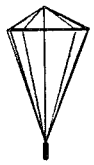
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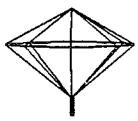
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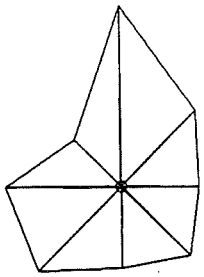
Figure B.2 Projected Crown Areas of the 18 Sample Trees oriented with magnetic north radii tword top of page. As an example of size, the east west diameter of tree #1 is 8.4m.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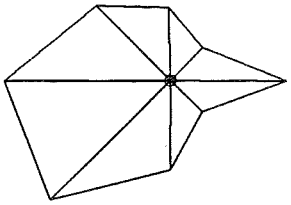
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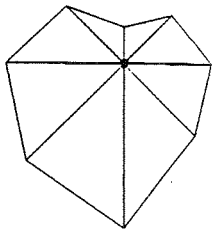
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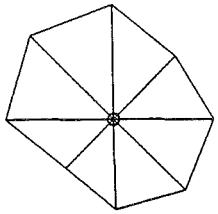
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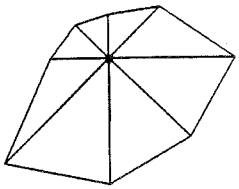
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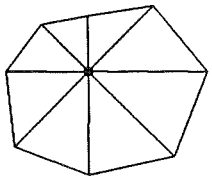
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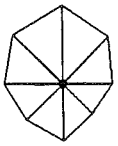
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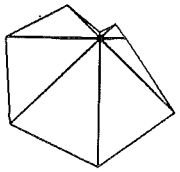
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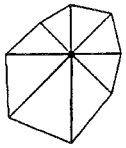
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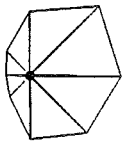
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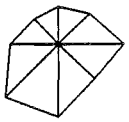
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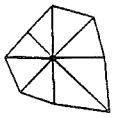
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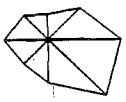
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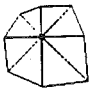
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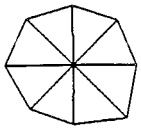
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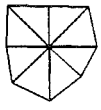
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APPENDIX C

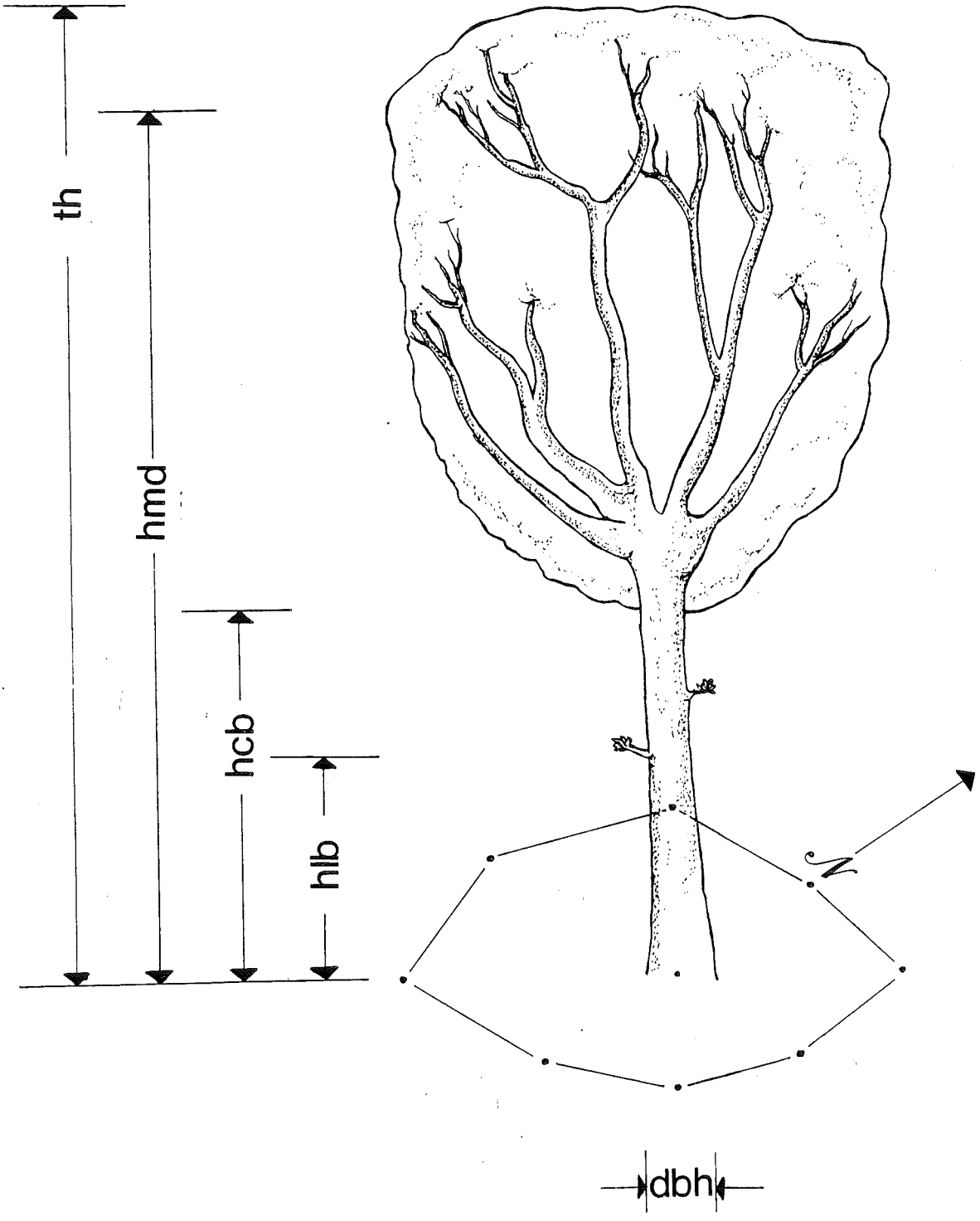

Figure C.1 Pre-Harvest Dimensions

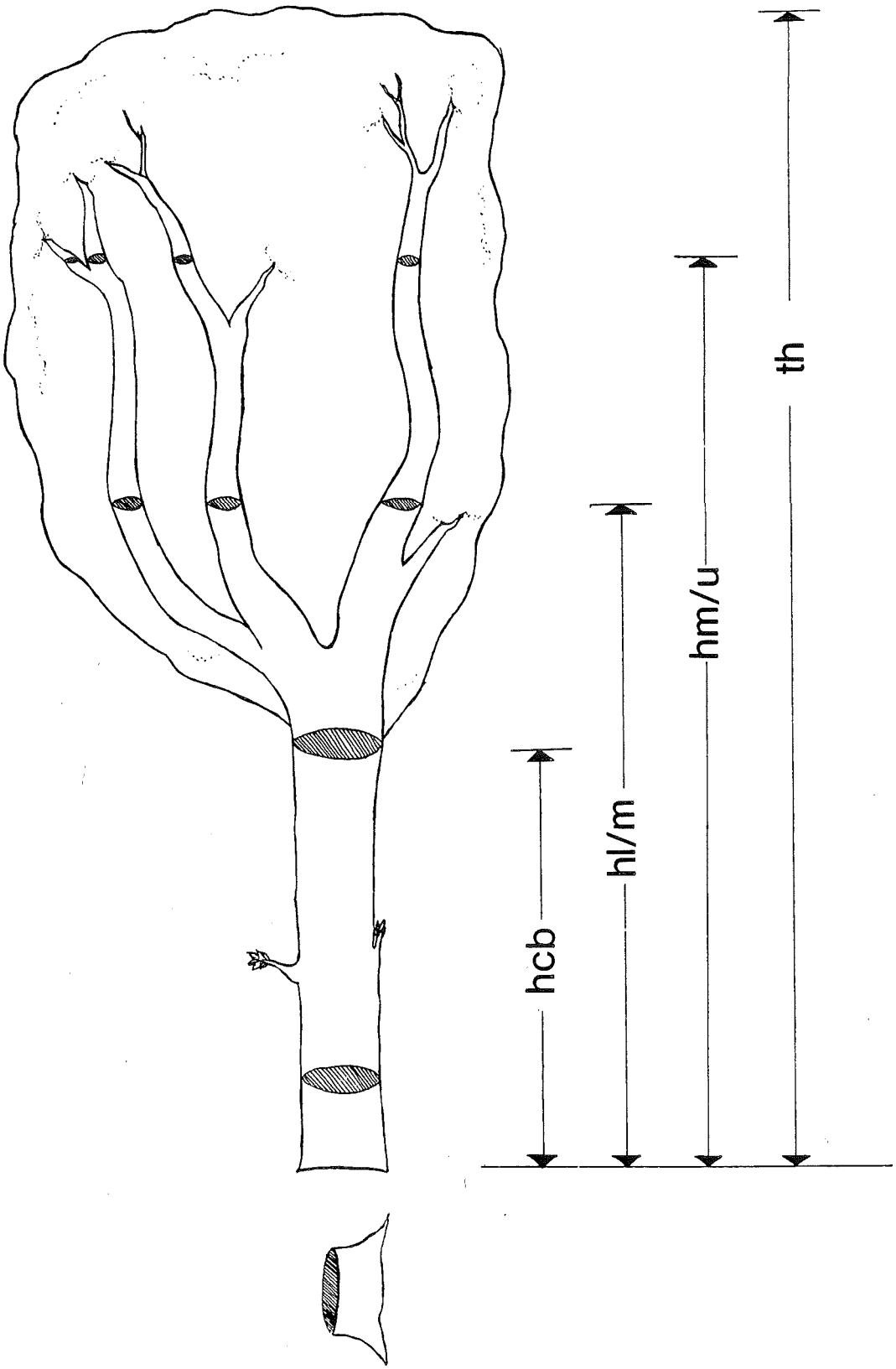

Figure C.2 Post-Harvest Dimensions

APPENDIX D

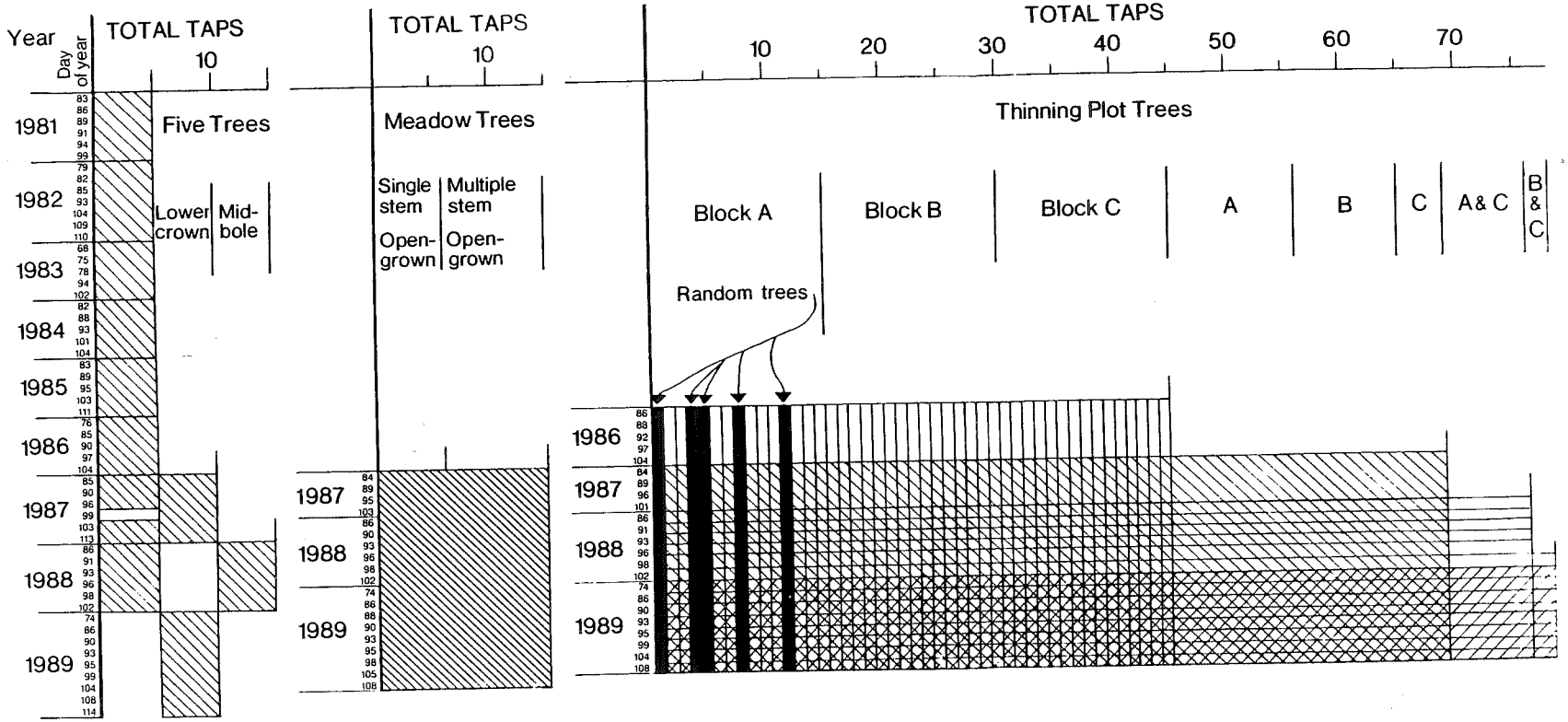

Figure D.1 Sap samples by plot, year, and time

APPENDIX E:

Manuscript of Techniques Paper
Prepared for Submission to
The Northern Journal of Applied Forestry

An Improved Canopy Access Technique[1]

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1 This research was supported by USDA, MacIntire-Stennis Forestry Research Program and the Kieckhefer Adirondack Research Fellowship

An Improved Canopy Access Technique

ABSTRACT Several canopy access techniques are reviewed including a preferred method that is presented in detail. Included is a description for devising the necessary equipment and step-by-step instruction for its use. The technique was developed for use with sugar maple with a crown base 40 to 50 ft. above the ground. A combination of mountaineering, hunting and fishing equipment and techniques is employed to propel an initial line into the canopy and rig the tree so that a rope can be ascended. Based on several years of development and testing, the technique is assessed with regard to possible variations and other techniques. The method should be most useful for practitioners and researchers working in the crowns of mature, stand-grown hardwood tree species like those found in the northeastern and midwestern North America.

Trees can grow to be extremely large organisms that can pose equally large problems for those attempting to study them. This is particularly true if one wishes to investigate them either below-ground or high in the canopy above-ground. Researchers in Idaho have recently reported on a technique that employs the careful use of explosives to excavate root systems (Bertagnole and Partridge, 1988). Such work is extremely important because it should encourage new research to be performed in an area that has all too often been simply ignored because of the difficulty involved in collecting data. Similarly, research within the crowns of mature trees has also been very limited and researchers more often prefer to study seedlings or saplings and extrapolate their results to large, forest-grown trees.

In this paper we present an inexpensive and relatively safe and easy method for exploring the above-ground world of the forest canopy. The method employs a combination of mountain climbing, hunting and fishing techniques and equipment to propel a line high into the crown and provide for rigging and access by the climber who ascends a rope. The basic technique was probably first used in tropical rainforests of central America by Perry (1984) and others who were studying pollination and other plant and animal interactions in this diverse ecosystem. Their techniques have been steadily improved to the point that a small cable car is presently in use. Nadkarni (1981) was probably responsible for bringing the technique to the temperate-zone were she studied canopy roots of big leaf maple

in rainforests of the Olympic Peninsula in comparison to those of the tropics. A similar and equally effective technique was developed for use in old-growth Douglas-fir forests of the Oregon Cascade Mountains (Denison et al., 1972). The architecture of these trees requires that lag bolts and steel hangars be fixed along the bole hence it is considerably more time consuming and potentially damaging to the tree and is considered less desirable unless completely necessary.

One of the most common methods for canopy access by researchers is scaffolding or steel towers as employed by Jurik et al. (1985) in mixed deciduous forests of Michigan's upper peninsula. Meteorological studies have also employed a tramway system supported by steel towers for unmanned data collection (Leonard and Eschner 1968). These methods can be relatively expensive and much less versatile; however, in that the towers are largely stationary and can be moved only with great difficulty.

A variety of equipment is commercially available for tree climbing including climbing spurs and "tree bicycles" that are often employed by seed collectors particularly those working with southern pines in the southeastern United States. However, none of these methods are as safe, inexpensive, versatile, nondestructive or as effective as the one described here for working in mature stand-grown deciduous trees like those found in the northeastern United States.

The technique that is presented was developed as part of a project studying the ecophysiology of sugar maple and particular with reference to its sap production at breast height (4.5 ft.) and in the crown 30 to 50 ft. above the ground. During the course of a three-year study, several canopy access techniques were investigated. The following technique, which is described in detail, was the most successful of these. Results will be discussed comparing this and other techniques.

Methods and Materials

The most unique and perhaps the most crucial piece of equipment with this technique is a combination hunting sling and fishing reel, hereafter referred to as the sling-reel apparatus (fig. 1). The sling that was used was a "Wrist-Rocket", manufactured in Columbus Nebraska, but any hunting sling with a brace on the wrist or forearm could be adapted. One could also be devised with approximately 3 ft. of 5/16 in. diameter solid round aluminum alloy bar stock and 2 ft. of 5/16 in. outside diameter surgical tubing. What is most important is that the sling braces against the users wrist or fore arm providing a steady aim, which is critical for the placement of the initial line in the canopy.

The fishing reel used was an open-faced spinning reel with a deep spool 1 3/4 in. in diameter. A large variety of equipment is

available and others, particularly larger surf-casting reels, have also been known to be used effectively by other researchers (personal communication, M. Whitmer and S. Sargent 1988). Here, the most important detail is that the reel be open-faced to allow for the free flow of line. The reel should be filled to capacity with supple heavy gauge 20 lb. test line. The line is the attached to a 3/4 oz. to 1 oz. fishing weight with a secure fishing knot such as the "Trilene knot". It is also useful to attach a small piece of brightly colored plastic flagging to the weight to monitor its trajectory and placement in the crown.

The reel and sling were connected with a 2 1/2 inch metal bracket, 4 hose clamps and a shim split from a piece of 3/4 in. dowel (see fig. 1). The sling-reel apparatus can then be sighted in, so to speak, in an open area to gain experience with different combinations of projectile force, trajectory and weight to obtain the necessary accuracy at the appropriate range.

The necessary lines for the climbing apparatus include one or more 1/2 in. diameter nylon mountaineering ropes (each normally 165 feet in length) and an equal amount of lighter, braided nylon parachute cord. The amount of rope and cord needed depends largely on the height of the crown in question but should be approximately 2.5 times the height of the canopy that is to be accessed. A temporary connection between the monofilament and the parachute cord

and a more permanent one between the parachute cord and the climbing rope can each be made with a one foot length of medium gauge steel wire and duct tape. The wire is tightly bent to almost 360 degrees and the two ends laterally taped to the larger of the two lines with the smaller line tied into the small exposed bend of wire. In the case of the cord and the climbing rope, the whole connection is further covered with additional tape. Experience has shown that it is important to make these connections using a rigid wire yet as narrow and as smooth as possible so as to allow for their easy passage through narrow branch forks. The two climbing ropes can simply be joined by a double fisherman's knot for if they are long enough they need not pass through the crown.

The remainder of the necessary equipment and techniques is drawn almost entirely from direct aid rock climbing technology (Peters 1982). These include a seat harness, a helmet, a pair of jumars or ascenders with etriers or foot stirrups attached, a repelling device, a belay plate and an assortment of 5 to 10 screw-gate carabineers and tubular nylon webbing slings of various lengths depending on the diameter of the trees to be climbed and limbs utilized. It should be emphasized that the actual equipment selection and at least the initial execution of the technique is best performed with the assistance of an experienced rock climber or mountain guide familiar with these techniques. Such people can be found working in affiliation with college outdoor programs and outing clubs

nationwide.

Once the equipment and expertise have been assembled the basic canopy access technique within the forest proceeds in four basic steps (fig. 2).

1) The selection of an appropriate branch system and the placement of the initial monofilament line into the crown using the sling-reel apparatus. Normally, the crotch of a healthy major branch or fork in the main stem is chosen to provide a large target for placement and a strong support for climbing. The weight or projectile should be fired with just enough force to get it over the desired branch while encumbering as few other branches as possible. A high angle of approach tends to minimize interference from branches and other trees.

2) Rigging the fixed climbing rope into the crown. This evolves removing the weight from the monofilament line and reattaching the line to the wire loop on the parachute cord. Then by reeling and pulling the successively larger lines can be placed in the canopy. Finally the free end of the climbing ropes can be secured to another tree or other suitable anchor by an assistant on the ground.

3) Ascending the climbing rope into the crown. Weight is alternately placed on each ascender with its corresponding foot stirrup as the other is moved progressively up the fixed rope. Secure protection and comfortable resting position is provided by the seat harness which is also attached to the ascenders. Once within the canopy further protection is set up with nylon slings before measurement or sample collection begins.

4) Descending from the canopy. This is achieved by the climber first shifting his/her weight to the fixed protection in the canopy while the assistant on the ground unties the fixed anchor and holds it fast with the aid of a securely anchored belay plate. The climber's weight can then be shifted back to the climbing rope while the fixed protection within the canopy is removed after which the assistant on the ground can slowly pay out the rope slowly lowering the climber to the ground.

RESULTS AND DISCUSSION

Once the technique described above was perfected, it proceeded quite smoothly with the actual time for accessing and descending the canopy, minus the time for data collection, being approximately one hour per tree. The time required for successive climbs is greatly reduced if a line is left in the canopy to facilitate rigging. Climbing spurs would be faster but their repeated use in any research

setting would be damaging particularly with thin barked species or, as in our case, where the xylem sap is under positive pressure causing profuse exudation. Perhaps the most important advantage of this technique is the safety that it provides the climber. No technique is ever completely safe but neither the climbing spurs nor any other climbing techniques discussed provides the protection of a properly rigged climbing rope.

Tree form and crown morphology is what largely dictates the necessity for, and the success of, any canopy access technique. Stand-grown trees with high crowns and long virtually branchless boles make climbing particularly difficult. If the crowns were closer to the ground, then one could simply use a large extension ladder to reach the lower branches. If there is a long bole with only a few epicormic branches, then not only are they not useful for canopy access but they also preclude the use techniques such as a "tree bicycle" that surround the main stem.

To move radially outward from the main stem or horizontally along a branch, it is safest to rig an aerial runway between two or more trees on which the researcher can move with a pulley attached to a seat harness (Perry, 1984). The largest limitation of any climbing technique is the extreme upper crown where branches are too small to provide support. Access to this environment is necessary for example to make measurements of photosynthesis on the exposed sun

leaves of the upper canopy. In such a situation, scaffolding and steel towers will remain a necessity.

Several variations are possible on the equipment and technique as described. A commercial version of the sling-reel apparatus is available through forestry equipment suppliers; however, its cost is approximately 10 times that of the one described including the cost of labor. Geysel (1960) developed similar equipment using a 40-pound bow fitted with a bow fishing reel but his climbing technique did not use jumars or other modern rock climbing technology.

The sling-reel apparatus can be eliminated all together by a technique which uses nylon slings tied around the bole as protection and climbing on them by using foot stirrups. If a nylon sling is looped around the bole and through itself, it tightens up when weight is applied. With this technique, it is important to use the softer tubular nylon sling material as opposed to the harder flat nylon webbing to provide sufficient grip via friction with the stem bark. Once in the crown the climber can then rappel down with the aid of a climbing rope. This technique is most similar to the one used by Denison et al. (1973) on Douglas-fir; however the nylon slings are used in place of the lag bolts and steel hangars for protection. The technique was tried on several large sugar maples but found to be extremely tiring and time consuming. It does; however, serve to demonstrate the effectiveness of the sling-reel apparatus used in conjunction with a fixed climbing rope and modern rock climbing

technology.

APPLICATIONS

This technique should be most useful to researchers needing to work in the lower to mid crown of trees with elevated canopies and a broad spreading main stem, such as the broadleaved species in the northeastern and midwestern United States. This would applicable to forest geneticists and others collecting seed, forest ecophysiologists, mycologists and others studying plant epiphytes, and zoologist, investigating the population dynamics and behavior of insects and arboreal vertebrates.

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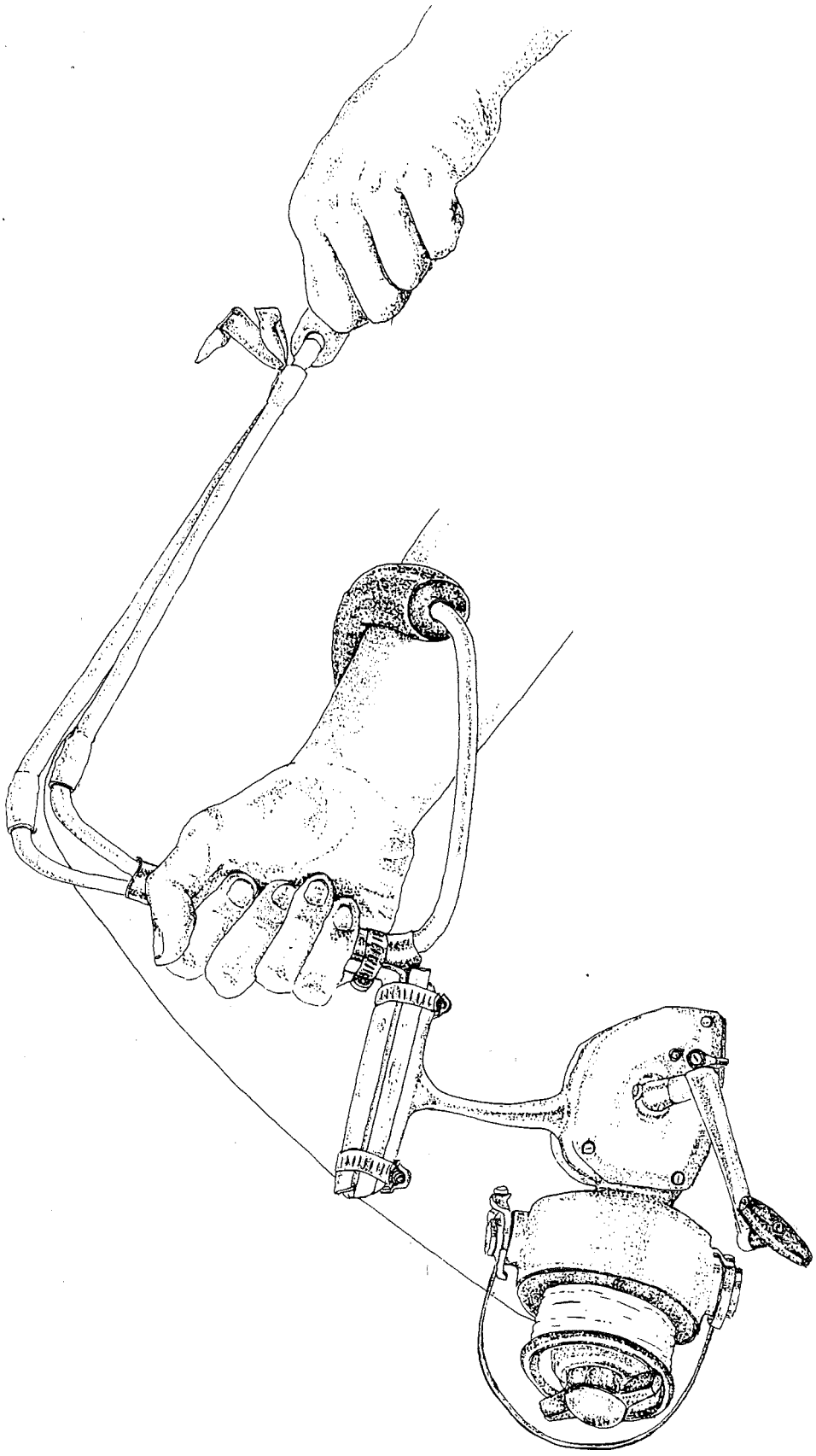
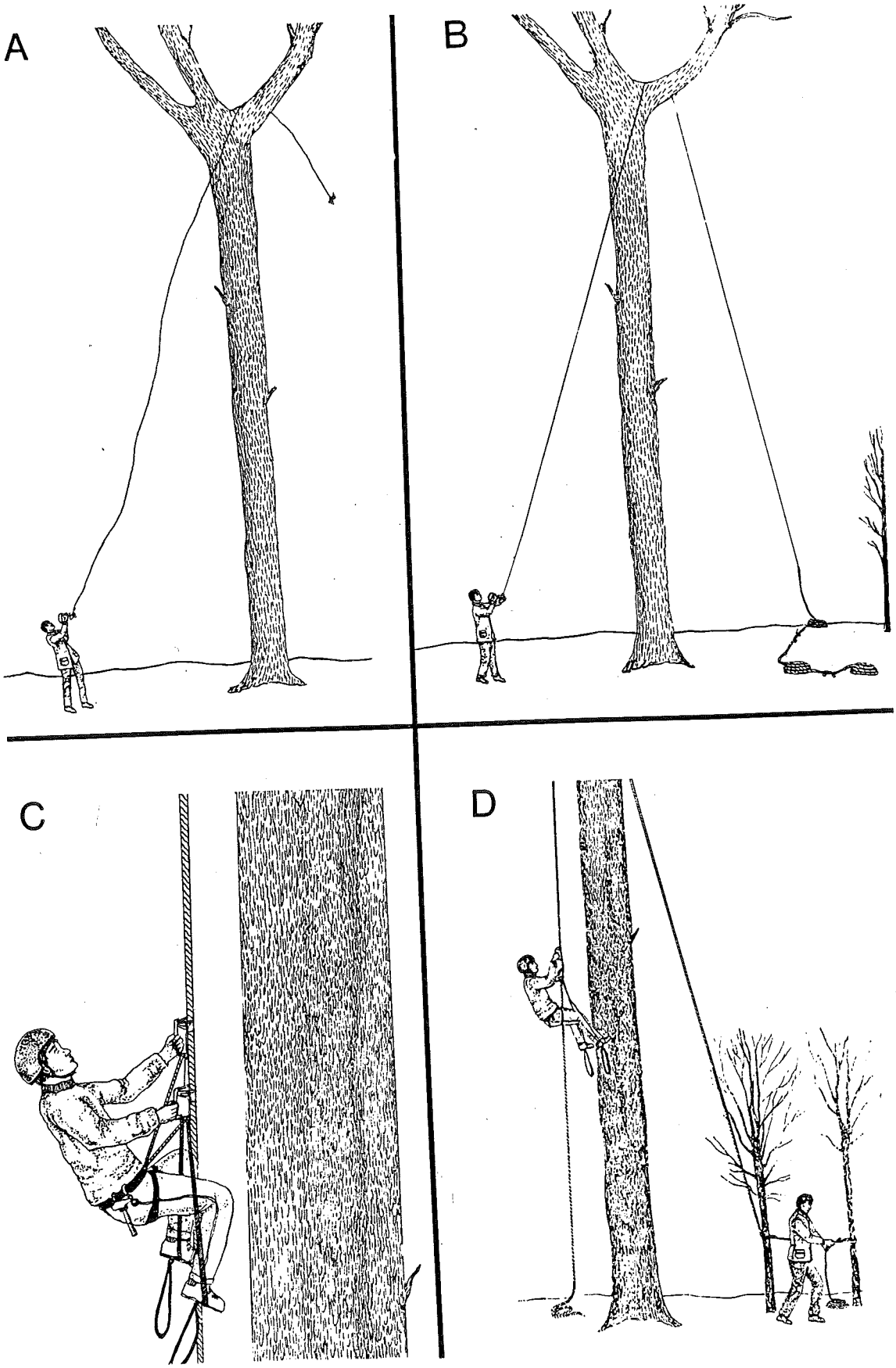


Figure E.1 The sling-reel apparatus which is devised from a hunting sling shot and an open faced fishing reel.

Figure E.2 Canopy Access Procedure: a)The selection of an appropriate branch system and the placement of the initial monofilament line into the crown using the sling-reel apparatus. b)Rigging the fixed climbing rope into the crown. c) Ascending the climbing rope. d) Descending from the canopy. (see text for further detail)


A
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APPENDIX F: Analysis of Gregory and Hawley (1983) Data Regarding Tap Aspect

TREE NO.	SAMPLE	RANKING OF PERCENT SUGAR (4 = HIGHEST, 1 = LOWEST) NORTH	EAST	SOUTH	WEST
1	INITIAL	4	3	2	1
2	INITIAL	3	1	2	4
3	INITIAL	3	1	2	4
4	INITIAL	3.5	3.5	1	2
5	INITIAL	1.5	3.5	3.5	1.5
6	INITIAL	2	3.5	3.5	1
7	INITIAL	4	1	2	3
8	INITIAL	4	1.5	1.5	3
9	INITIAL	2	3	1	4
10	INITIAL	2.5	1	2.5	4
11	INITIAL	2.5	1	2.5	4
12	INITIAL	2.5	4	2.5	1
13	INITIAL	2	3	1	4
14	INITIAL	1	3	4	2
15	INITIAL	3	2	4	1
1	1 HOUR	2	3.5	3.5	1
2	1 HOUR	2.5	2.5	1	4
3	1 HOUR	3	1	2	4
4	1 HOUR	3	2	4	1
5	1 HOUR	1	4	3	2
6	1 HOUR	2	3.5	3.5	1
7	1 HOUR	4	1.5	1.5	3
8	1 HOUR	2.5	2.5	1	4
9	1 HOUR	1	3	4	2
10	1 HOUR	1.5	3	4	1.5
11	1 HOUR	2.5	4	2.5	1
12	1 HOUR	4	3	1	2
13	1 HOUR	2.5	4	2.5	1
14	1 HOUR	1	3.5	3.5	2
15	1 HOUR	4	2	3	1
MEAN		2.566666	2.6	2.5	2.333333
S.D.		0.963788	1.044030	1.056724	1.240519
95% C.I.		0.344887	0.373601	0.378144	0.443914

APPENDIX G:
Abstract of Paper Presented at the
First Conference on Agroforestry in
North America,
August 13-16, 1989
University of Guelph
Guelph, Ontario

THE GEOGRAPHICAL DISTRIBUTION OF FREEZE-THAW CONDITIONS AS AN INDICATOR OF THE RELATIVE POTENTIAL FOR MAPLE SUGAR HARVESTING

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Positive xylem pressure induced by freeze-thaw cycles in air temperature has long been recognized as the driving force in maple sap flow. Variation in these phenomena is in turn regulated by the time of year, latitude, elevation and the proximity of large bodies of water relative to the location of interest. Data on maximum-minimum air temperature gathered during a 30-year period from stations throughout the range of sugar maple (Acer saccharum Marsh.) is being analyzed to develop a mapping of the incidence of winter and springtime freeze-thaw conditions in both the United States and Canada. It is hoped that this information, in conjunction with data on soils and growing stock density will be useful to extensionists and others interested in the development of the maple syrup industry.

APPENDIX H

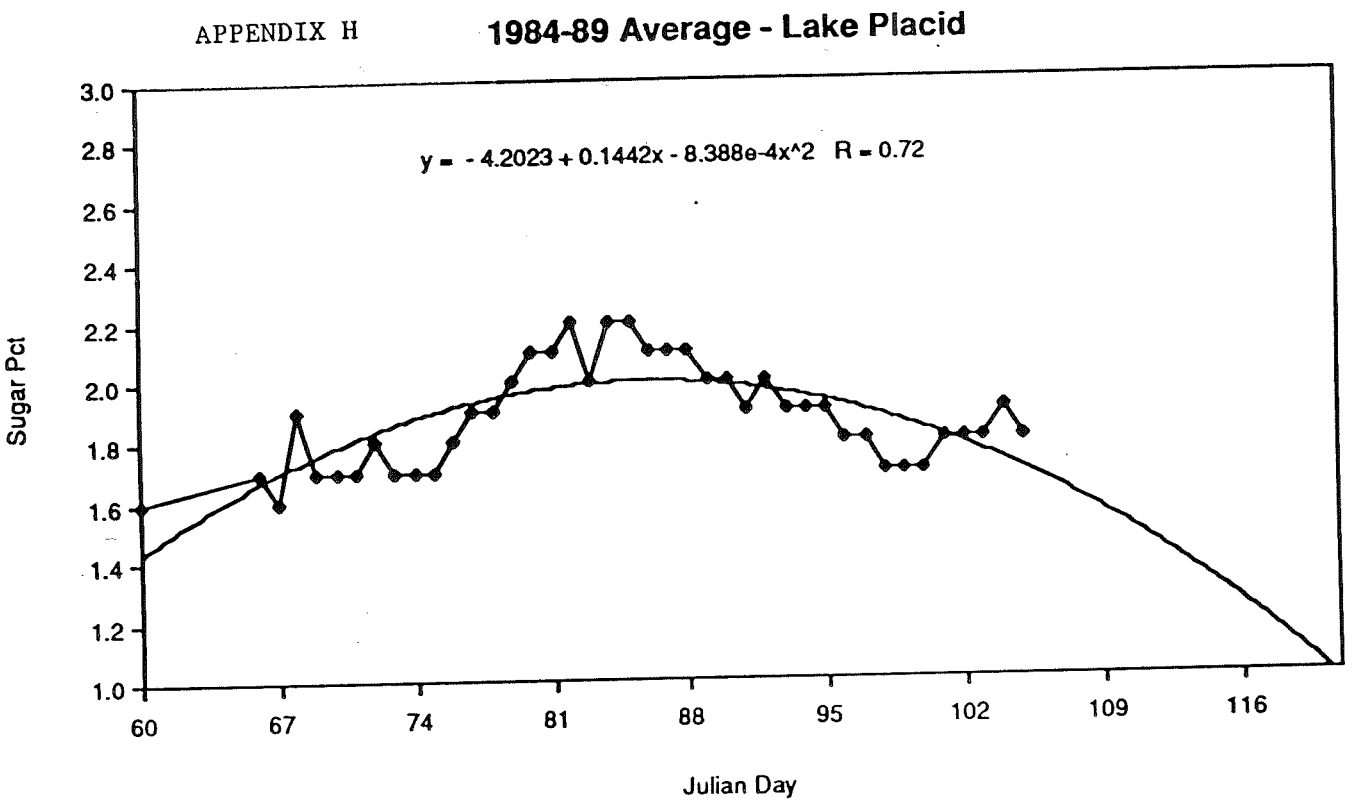

Figure H.1 1984-1989 Average Sap Sugar Concentration Versus Julian Day For Uihlein-Cornell Sugarbush, Lake Placid New York (Courtesy of L.J. Staats and K.L. Eggleston)

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